

OBSERVATIONS ON THE SCRATCH-REFLEX IN THE SPINAL DOG. BY C. S. SHERRINGTON. (27 Figures in Text.)

(The Physiology Laboratory, University of Liverpool.)

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I. THE RHYTHM OF THE REFLEX RESPONSE IS INDEPENDENT OF THE RHYTHM OF THE STIMULUS.

THE scratch-reflex of the 'spinal' dog can be elicited by electrical stimuli¹ as well as by mechanical of the kinds previously described² as efficient for it. It was noted in a former paper³ that the frequency of the rhythmic response of this reflex is not sensibly affected by the rate of repetition of mechanical stimuli evoking it. For testing this relation electrical stimuli possess advantages over mechanical. With the former the rate of application, duration, &c., can be better adjusted and controlled. If a graphic record of the scratching movement itself be taken simultaneously with that of the application of the stimuli to the skin, the rhythms of the movement and of the stimulus can be compared.

¹ *Proc. Physiol. Soc.* xvii. 1904. (This *Journal*, xxxi.)

² This *Journal*, xxx. p. 39. 1903.

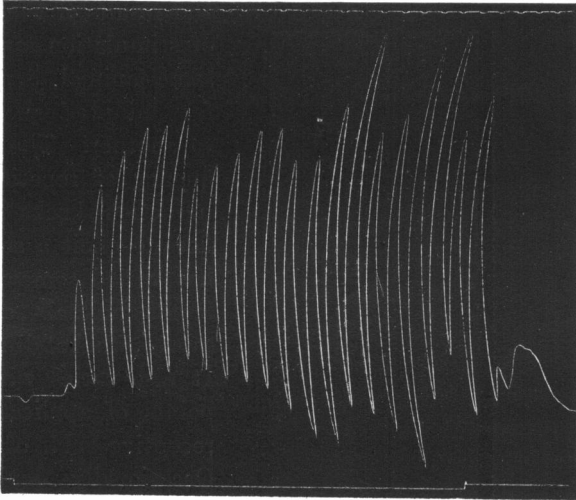
³ This *Journal*, xxix. p. 64. 1903.

As to the forms of electrical stimulation which are effective for provoking the reflex, the constant current, faradism, and the high-frequency discharge are all found to be so, but faradic currents are what I have used most often. To apply them the point of a fine entomological pin, preferably gilt, has been lightly inserted in the skin to a depth of about one millimetre or less. The pin can be made the kathode for delivering series of single shocks, and is a useful stigmatic electrode for series of double shocks; the other electrode is made diffuse (a large copper plate) and applied to the shaven and moistened skin somewhere headward of the spinal transection. Feeble induced currents with the secondary coil of the Bern inductorium beyond the lowest mark on the Kronecker scale and imperceptible to the tongue-tip will often evoke the reflex if the reflex conditions of the spinal cord be good.

Electrical stimuli, although they answer well as a rule for the ordinary purposes of experiment with the scratch-reflex, are nevertheless distinctly less effective than those mechanical previously described as specially appropriate to the reflex. Probably the latter are the really *adequate* stimuli. The relative inefficiency of the electrical stimuli is clearly brought out when the spinal condition is such that the reflex is less easily elicitable than usual. The electrical stimuli will then, even when of full strength, often altogether fail to provoke the reflex, while mechanical stimuli still provoke it. Thus in the period during which the animal is slowly recovering from 'spinal shock' consequent on the spinal transection, it may not be until long after the reflex has become demonstrable by mechanical stimuli that electrical become able to evoke it. The less efficiency of the electrical stimulation is also well shown with excitation in the border zone of the skin-area whence the reflex can be evoked (Fig. 19). There the threshold-value of stimulus is higher than in most other parts of the field, and though rubbing with the finger or a pencil-point fairly easily excites it, the faradic or galvanic current may quite fail to do so, even when intense. Of all forms of electrical stimulation the most effective in my experience is high-frequency discharge, even though applied without actual contact with the skin. Where mechanical stimulation fails to excite the reflex I have never found any electrical stimulation succeed.

The rhythmic scratching movement of the hind limb can be examined in several ways. Thus, the flexion at the hip can be recorded (Fig. 1) by attaching to the thigh above the knee a thread operating on a light lever. Falsification of the period of the rhythm by the periodicity of the recording lever has been controlled by varying the length of the lever, and by in certain instances dispensing with the lever and allowing a bristle, tied into the recording thread, to inscribe the movement. These measures gave records in all cases exhibiting the same rhythm.

If each separate flexion of the limb is called a beat, the scratching movement of the limb shows a frequency of about 4·8 beats per second. The frequency of the rhythmic movement is, however, not always exactly the same; its variation in my records lies for the most part between the limits of 4·4 and 5·2 beats per second. The earlier beats in a reflex often follow each other rather more rapidly than do the later in the series.



All the tracings in the figures read from left to right.

Fig. 1. Scratch-reflex elicited by unipolar faradisation. Signal below. Time in fifths of seconds above.

In all of the considerable number of dogs examined in this research the rate of rhythm of the beat has been practically the same. In some of these animals the spinal transection had been in the posterior cervical region, in others as far back as the 10th thoracic segment. From one of the animals graphic records have been taken from time to time over a period of two years and three months, and the rate and general features of the rhythmic movement have been found to remain practically unaltered throughout that time.

In a dog in which a liberal semisection in the middle of the cervical region had been established the reflex became elicitable on the side of the semisection, as often happens after liberal semisection. It was elicitable not only from the saddle-shaped field of skin regularly revealed (Fig. 19) as the receptive field by posterior cervical transection, but also from the dorsal aspect of the neck behind the semisection. The reflex in this case was also elicitable from the foremost nipple. The rate of the rhythm of the movement when excited from the dorsal skin was found in this animal to be habitually quicker than

usual, *i.e.* usually 5·4 beats per second. When excited from the nipple the reflex was particularly brisk, and had a frequency much higher still, *e.g.* on several occasions 7·4 beats per second. I have not met with nearly so high frequency as this in any other examples of the reflex. No other characters in this example supported the suspicion that it was really some other reflex than the ordinary scratch-reflex.

The rhythm of the reflex movement as excited by electrical stimulation fully resembles that obtaining under mechanical. Fig. 2 shows

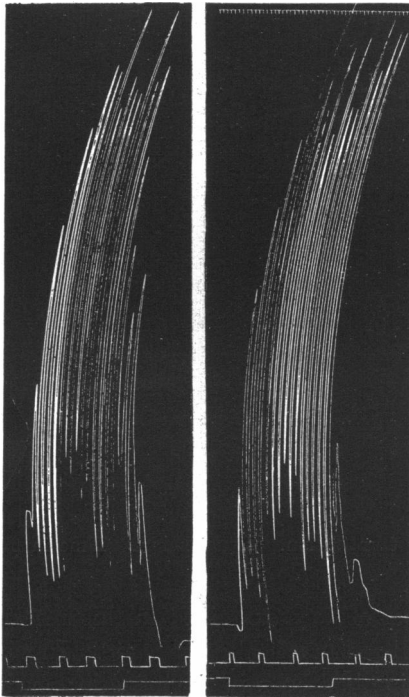


Fig. 2. Scratch-reflexes elicited by mechanical stimulation *A*, and by electrical (unipolar faradisation) *B*, respectively. Bottom line signals duration of stimulus. Time in seconds next above. At top in *B* is the record of delivery of the induction shocks, 8 a second.

the results of the two modes of stimulation applied in the same animal and within a few minutes' succession one to another. The lowest frequency of repetition of the induction-shocks which suffices to elicit a scratch-reflex has varied somewhat in different animals and in the same animal at different times. It also varies with different points of application in the receptive-field of the skin. Occasionally double shocks following each other in series at the long interval 1·6 sec. between double shock and double shock have been successful, but the rhythmic reflex movement so obtained although excited and just maintained has tended to be somewhat irregular and 'groupy' as if on the point of failing at short intervals. Double shocks ·91 sec. and ·88 sec. apart have been more frequently successful, and

shocks ·77 sec. and ·66 sec. apart are more successful still. Shocks at an interval of ·5 sec. have been uniformly successful, but shocks at ·33 sec. interval excite more quickly and with the secondary coil at greater distance from the primary. Shorter intervals employed with double-

shocks have been .28 sec., .1 sec., .05 sec., and .01 sec.; all these excite the reflex well. The reflex has also been easily and regularly excited with double shocks when the interruptor in the primary circuit was a tuning-fork (Zimmermann) of 512 d. v. per second. On the supposition that this really supplied an effective double shock at each vibration the interval between the stimuli became less than 2σ . With this stimulation the reflex though quickly evoked and maintained regularly for a time tended to rapidly die out.

Under all these different rates of stimulation the frequency of the rhythm of the resulting reflex movement remained practically the same, namely, about 4.8 beats per sec. Similarly with series of single shocks, make or break. With single shocks the observations have included intervals from shock to shock varying from .5 sec. to .02 sec. The variation of rate has been obtained with rotating keys in the primary circuit, especially with Engelmann's polyrheotome (Kaguenaar) and with Brodie's rotating key driven by an electro-motor. Slight differences in the rate of rhythm observable in the records of the reflex movement appear related to other conditions of experiment—*e.g.* to intensity of stimulation, to spinal excitability, &c.—rather than to the frequency of the exciting stimuli applied. Apart from these slight differences the rate of rhythm of the movement has been the same throughout.

Further, the reflex movement has been initiated by single shocks at 6 per sec. and then continued and maintained by double shocks at 512 per sec., and under this change in the rate of application of the stimuli the rate of rhythm of the reflex movement has remained unaltered, namely, 4.8 per second. With Engelmann's polyrheotome it is easy without altering the rapidity of the opening and closing of the key to make the intervals between the successive delivery of the induced currents unequal, thus distributing them in more or less irregular groups. For instance after a few observations with stimuli following regularly at 20 per second each third peg is removed from the rheotome, or each third and fourth peg. The stimuli in the latter case follow with 50σ interval between one pair and with 150σ interval between the next pair. In spite of these irregularities of interval in the application of the stimuli if no interval, with fairly strong stimuli, exceeds about 1 full second, the rhythm of the reflex movement persists unaltered, namely, with a frequency of about 4.8 beats per sec. and is as regular as if the exciting stimuli proceeded at regular intervals. With the interposition of intervals above 1 sec. the reflex shows signs of lapsing just after the interposition of that interval, that is, it tends to become 'groupy.'

Further, the rhythm of the reflex response to high frequency discharge (Fig. 3) is the same as in the above cases. And the reflex when evoked by the constant current has also the same rhythm. With the constant current applied so that a diffuse anode lies outside the receptive skin-field and headward of the spinal transection while a stigmatic kathode

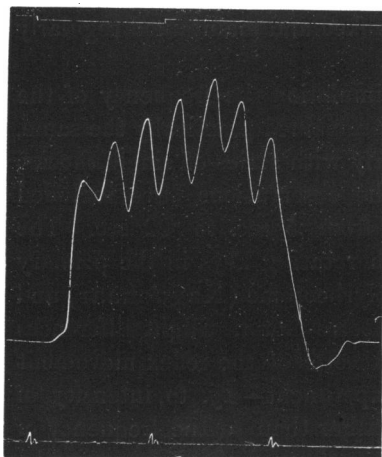


Fig. 3.

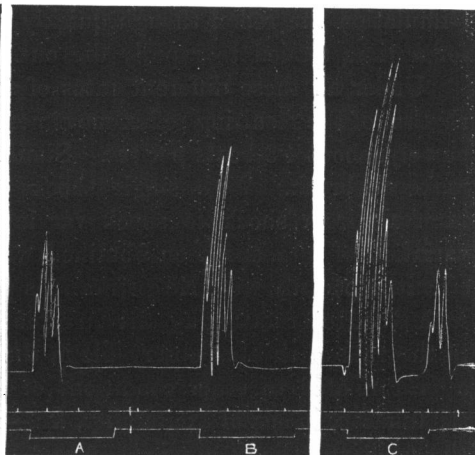


Fig. 4.

Fig. 3. Scratch-reflex evoked by high frequency discharge. Signal above. Time in seconds below. In this animal the threshold value of stimulus was high at the time of the observation.

Fig. 4 A, B, C. Scratch-reflexes excited at the kathode of a galvanic current. The strength of the current was greater in B than in A, in C than in B. Signal below.

acts in the receptive field the reflex appears at make of the current (1.5 milleamperes) and lapses (Fig. 4 A). With more current the reflex appears at make, then lapses, and reappears at break (Fig. 4 C). With more current still the reflex is maintained for a short time during the passage of the current and is then intensified on cessation of the current.

As shown previously¹ a heat-beam brought to bear on the skin within the receptive-field will excite the reflex. This can be considered to form like the galvanic current a more or less constant continuous stimulus. The rate of rhythm of the reflex as excited by the heat-beam is the same the reflex shows when provoked by the other forms of stimulation.

It seems therefore that "this reflex arc resembles the cardiac

¹ This *Journal*, xxx. p. 39. 1903.

mechanism in responding to a constant stimulus rhythmically¹, and that modifications of the external stimulation "hardly appreciably affect the frequency of that rhythm?" The reaction of the reflex mechanism exhibits therefore in a marked degree the phenomenon of 'refractory phase.'

As to the rate of rhythm of the scratch-reflex in comparison with that of other rhythmic movements in the dog, it is about half as fast as that of the ankle-clonus, sometimes observable in the spinal dog, of which I have obtained records from some of the same animals that have yielded records of the scratch-reflex. It is also about half as fast as a rhythmic clonus I have often obtained records of in the after-discharge of the flexion-reflex in the dog. On the other hand, it is about twice as fast in rate as a rhythmic stepping movement of the hind leg (Fig. 5)

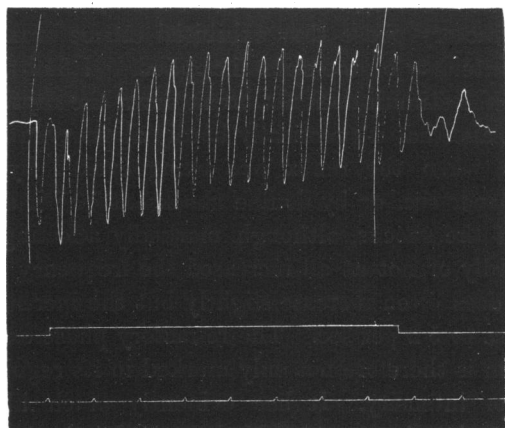


Fig. 5. The crossed stepping-reflex, excited by unipolar faradisation of the opposite hind foot. Time in secs. The signal line above the time line.

which I find elicitable in the spinal dog by faradic stimulation of the opposite hind foot—a reflex which may be termed the 'crossed stepping reflex.' It is also about twice as fast as the 'mark-time' movement which occurs (Goltz and Freusberg) in the spinal dog when the animal is held up free from the ground with the hind limbs pendent. But the rate of rhythms of this latter reflex, in my experience, varies much in different animals and at different times, and Philippson's² chronography of the kindred rhythmic movements of trot and gallop in

¹ *Proc. Physiol. Soc.* p. xvii. 1904 (this *Journal*, xxxi).

² Heger's *Travaux de Laboratoire*, Institut Solvay, Bruxelles. 1905.

the spinal dog exemplifies the same. The rate of the rhythm of the scratch-reflex in the dog is closely similar to that found by Gotch and Burch¹ as average for the rhythmic reflex response of the giant nerve-cell supplying the electric organ of *Malapterurus*. But the reflex rhythm in the scratch-reflex is much less variable in frequency² than is that of the discharge of the nerve-cell of *Malapterurus*.

II. REFRACTORY PHASE.

The scratch-reflex gives a rhythmic response to a constant stimulus and to stimuli following in series quicker than its own rhythm or at rhythms whose time-relations must interfere with its own. It therefore behaves as though at recurrent periods it, so to say, paid no regard to a stimulus that would otherwise excite it. There remains to examine whether its refractory phase thus exhibited can be broken through by increasing the intensity of the stimuli applied. I find that increase of the intensity of the stimuli does not break down the rhythmic character of the response, and that it practically hardly alters even the rate of the rhythm. Thus, when the reflex was being evoked by break shocks delivered at 30 per sec. or by double shocks at 50 per sec., increase of the intensity of the shocks, although markedly affecting the reflex in other ways, hardly or not at all increased the frequency of its rhythm. The frequency does often increase slightly but the increase is small, *e.g.* from 4.6 per sec. to 5.2 per sec. The refractory phase exhibited by the reflex mechanism is therefore not only marked in its regularity, but also in its degree or intensity. It has evidently much likeness in this respect to the swimming-beat of *Medusa*, and indeed to the beat of the heart.

In regard to what portion of the reflex-arc of the scratch-reflex is responsible for the refractory phase the following considerations arise. Among the muscles which execute the reflex-movement may be included with certainty dorso-flexors of the ankle, flexors of the knee, and flexors of the hip. These muscles respond by tetanic and not by clonic contraction when their motor nerves are stimulated by stimuli at rates of 30 per sec. or more. Moreover they exhibit tetanic contraction when executing other spinal reflexes, *e.g.* the flexion-reflex of the limb. They and their motor nerves therefore though expressing the rhythm of the scratch-reflex

¹ *Proc. Roy. Soc. London.* 1899.

² Sherrington, *Proc. Physiol. Soc. cit. supra.*

cannot be regarded as its originators. They are not responsible for the refractory period exhibited. The brief contractions of the clonus of the scratch-reflex are, one may assume, short tetani, like those for instance of the diaphragm in the rhythmic movement of respiration.

At the other end—the receptive end—of the reflex-arc there seems little likelihood that the afferent nerve possesses a refractory period such as that exhibited in the reflex reaction. I have not as yet succeeded in obtaining the scratch-reflex by direct stimulation of an afferent nerve.

The difficulty of eliciting directly from the afferent nerve certain reflexes easily elicitable by stimulation of the skin is recognised. Marshall Hall¹ called attention to it. Goltz² never succeeded in eliciting the croak-reflex of the frog by any direct electrical excitation of the afferent nerves from the very skin whence it is readily obtained by the usual mechanical stimulus ('stroking'). Reflexes of nociceptive origin are easily elicitable by direct stimulation of afferent skin-nerves, but the scratch-reflex is not³ of purely nociceptive character, and purely nociceptive reflexes tend to inhibit it. The afferent nerves passing from the skin-region that yields the scratch-reflex contain rich quota of nociceptive afferent fibres. The direct stimulation of these nerve-trunks tends to produce a nociceptive reflex, and not the scratch-reflex. If the needle-point used as the stigmatic electrode for the scratch-reflex be inserted too deeply into the skin and a more than moderate intensity of excitation is used, another reflex, not the scratch-reflex, is excited.

Failure, therefore, to elicit the scratch-reflex by direct stimulation of afferent nerve-trunks does not appear remarkable. But the failure leaves open the possibility that the rhythm and refractory period are attributable to the receptive end-organs within the skin itself.

In a former paper⁴ evidence was given that the cutaneous nerve endings specially concerned in exciting the scratch-reflex are, in the dog at least, closely connected with the hair roots. Since then I have in regard to the large saddle-shaped area of hairy skin on shoulder and back met nothing controverting that evidence. But further acquaintance with the reflex shows that it is also elicitable from the nipple (Fig. 19), that is from skin practically devoid of hairs. The reflex has not been obtained from nipple in all the dogs examined; and only from certain nipples in those dogs in which the nipples have reacted. From the hindmost nipple I have not in any dog obtained the reaction easily; from the second nipple I have not obtained it at all. The dogs (bitches) in which the nipples have reacted have all, to judge from the appearance of the nipples, at some time suckled puppies. The nipples yielding the reaction were large and flaccid. The dogs not yielding the reaction from the nipples had none of them, with one possible exception, borne puppies.

The scratch-reflex as evoked by stimuli applied to the saddle-shaped area of dorsal skin

¹ *Memoirs on the Nervous System*, London. 1837.

² Gergens, *Pflüger's Archiv*, XIII. p. 61. 1876.

³ *This Journal*, xxx. p. 39. 1903.

⁴ *This Journal*, xxx. p. 39. 1903.

is unilateral and uncrossed; that is, the stimulus excites scratching movement only in the hind limb homonymous with the side stimulated. This uncrossed unilaterality holds less strictly for the nipple areas. With the fourth nipple (Fig. 19) irritation not seldom produces scratching movement in the *crossed* hind limb, though less easily than in the homonymous. In regard to this it may be remarked that the nipples lie accessible to reach by either hind paw, whereas the saddle-shaped dorsal area is accessible to the homonymous paw only.

There is, however, a feature in the scratch-reflex which seems to exclude the possibility that the rhythm and refractory period of the reflex response originate either in the receptive skin-organs or in the afferent nerve fibres of the reflex arc. If, while the reflex is being excited by, for instance, unipolar faradisation at a stigmatic pole inserted at a point *A* in the receptive skin-field, another point *B* in the

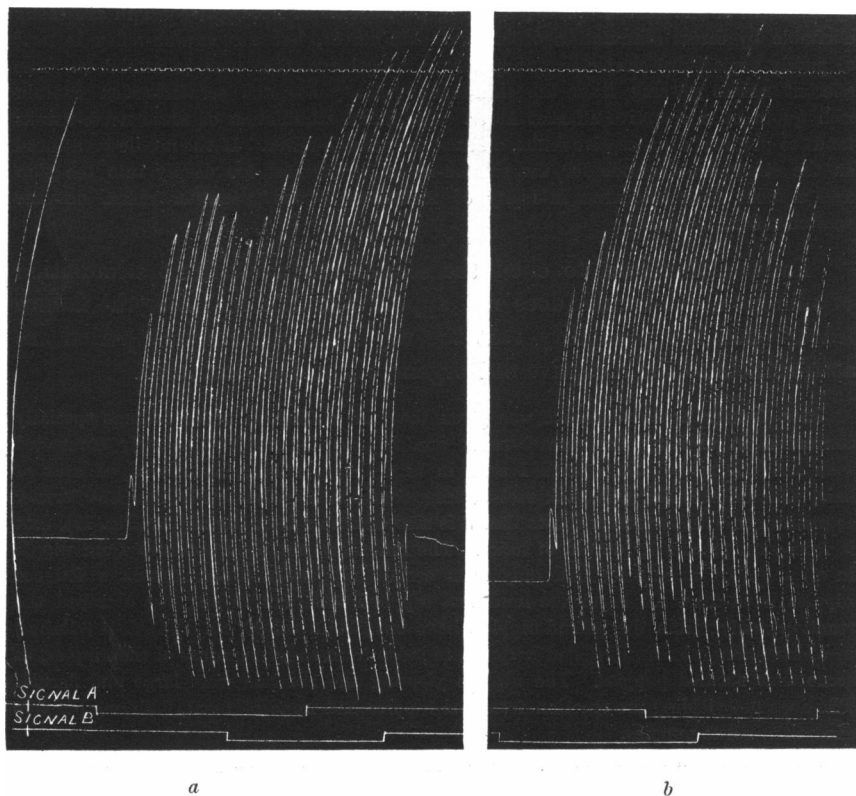


Fig. 6 *a, b.* (*a*) Scratch-reflex evoked by unipolar faradisation first at a point *A* and then continued at a point *B*. Signal *A* marks duration of stimulus at *A*; signal *B* that of stimulus at *B*. Time above in $\frac{1}{16}$ th secs. (*b*) Similar to *a*, but with the sequence of the stimulation at skin points *A* and *B* reversed, as shown below by the signals.

field, for instance 10 centimetres distant from *A*, be excited, the rhythmic reflex already in progress from *A* reveals no evidence of interference with the reflex elicited from *B* (Figs. 6 and 7). The rhythm of the second reflex does not interrupt, check, or engraft itself

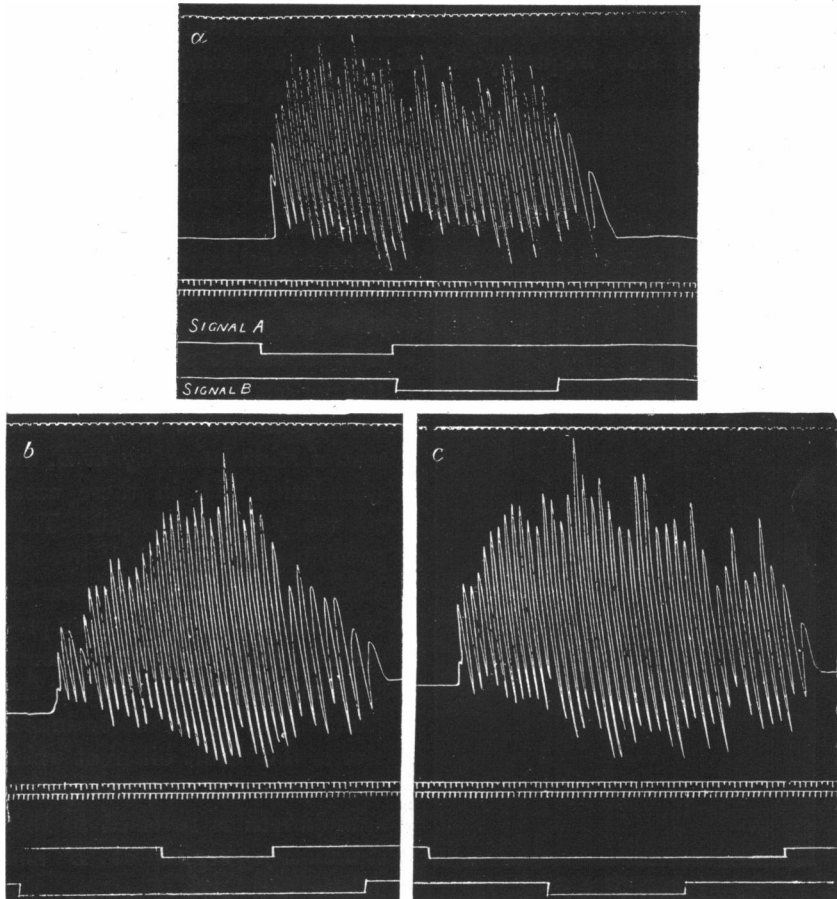


Fig. 7 *a*, *b*, *c*. Scratch-reflex excited by unipolar faradisation at two separate skin points *A* and *B*. Signals *A* and *B* show the moment and duration of the stimulus at these points respectively. The delivery of the shocks at each skin point is recorded in the lines *A* and *B* above the signals *A* and *B*. Time above in $\frac{1}{4}$ th secs. In Figure *a* the stimulation at *B* just succeeded that at *A*. In Figure *b* the stimulation at *A* was interpolated into the period of that at *B*; in Figure *c* the stimulation at *B* was similarly interpolated into that at *A*.

between the phases of the rhythm of the former reflex. It simply smoothly harmonises with it without any obvious disturbance of the rhythm. Since the motor apparatus in operation can reply by rhythms of contraction much faster than 4·8 per sec., and can indeed yield perfectly tetanic fusion of contractions, it might have been expected that the resultant reflex under the double initiation would show a rhythm of double the 4·8 per sec. frequency. That is not the result, nor is it even with relatively slow frequency of delivery of the exciting stimuli, *e.g.*

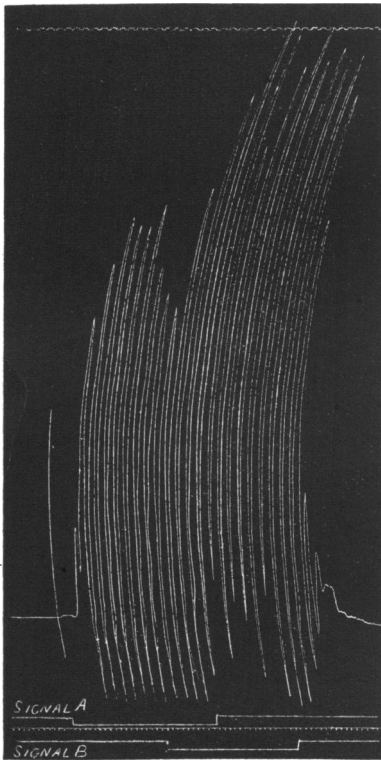


Fig. 8. Scratch-reflex elicited from two skin points *A* and *B*, the former of which gave the 'low' form of the reflex, the latter a 'high' form of the reflex. The rate of stimulation (unipolar faradisation) at *B* was also of a wholly different frequency from that at *A*. The slow succession of shocks employed at *A* is marked between the signal lines. Time in $\frac{1}{4}$ th secs. above.

7 per sec. allowing the shocks applied at the two seats of excitation to fall accurately alternately at the two places (Figs. 7, 9). Nor is the result altered by using a slow series of stimuli at one skin point and a rapid at the other (Fig. 8), *e.g.* serial stimuli of 7 per sec. at point *A* and of a 100 per sec. at point *B*. It might be suspected that at the second seat of stimulation, *e.g.* at *B*, the stimulation was in these cases not really effective at all. That possibility is excluded by the observation that the reflex started by excitation at *A*, and then proceeding under stimulation both at *A* and *B*, continues when the stimulus at *A* is discontinued. Nor is the result different when the sequence of the two separate stimulations is reversed so that stimulation begins at *B* and follows at *A*. Further, the rhythm of the stimuli at *A* and at *B* respectively may be made widely irregular; or the stimulation at *A* may be mechanical while that at *B* is electrical, or *vice versa*. The reflex rhythm persists unbroken, and smoothly

merges from one reflex into the other. If there is marked disparity between the intensities of stimulation at the two separate spots of provocation the rhythm of the reflex when the stronger stimulus is in operation may be rather quickened, *e.g.* become more than instead of less than 5 beats per sec., but there is no evidence of other disturbance or break in the rhythm.

Again, the scratch-reflex has a somewhat different form according as it is elicited from this or that point of the receptive field. From some points the reflex has more tonic contraction underlying its clonus. When, while the reflex is being elicited from one point a second point yielding the reflex in somewhat different form is excited, the result is obvious in the different form assumed by the reflex under its conjoint excitation. Yet here again no hitch in, or reduplication of, the rhythm appears (Fig. 9).

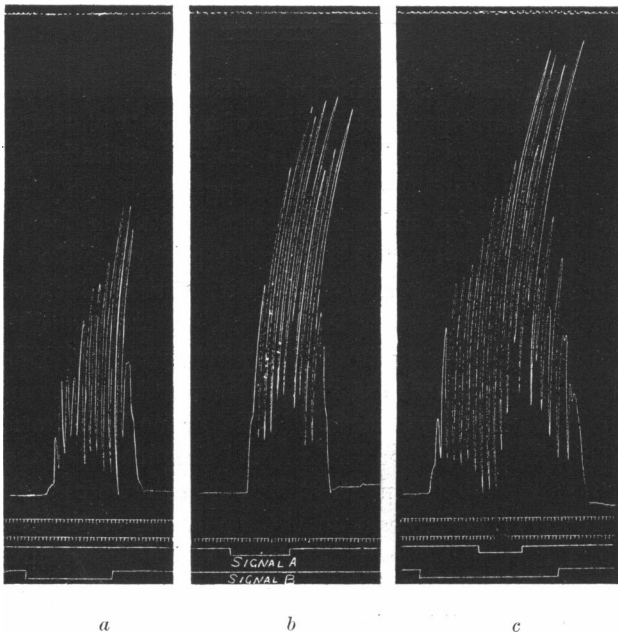


Fig. 9 *a, b, c.* Scratch-reflexes elicited *a* from a skin point *A*, *b* from a skin point *B*, *c* from skin points *A* and *B* with partially overlapping duration of the stimulations, but with the individual induction shocks of the two stimulations falling alternately at *A* and *B*. The moments of delivery of the induction shocks at *A* and *B* respectively are recorded in the two lines above the signal lines. Time in fifths of seconds. The character of the *B* reflex grafts itself upon that of the *A* reflex, but without break or reduplication or disturbance of the rhythm.

Hence it seems that the recurrent refractory phase of the reflex as elicited from a point *A* applies also to the stimuli delivered at point *B*¹. Similarly Zwaardemaker finds a refractory phase of reflex deglutition when induced by stimulation of superior laryngeal nerve of one side obtain also for stimuli applied through the laryngeal of the opposite side². The place of occurrence of the refractory phase must therefore in these reflex mechanisms lie in some element common to the reflexes initiated at *A* and *B* respectively. The reflex channels belonging to skin points *A* and *B* certainly do not before they enter the spinal cord impinge upon any such common mechanism. There can be excluded therefore from the seat of manufacture of the refractory phase both the afferent nerves and the receptive end-organs in the skin itself. The refractory phase is therefore of central (intraspinal) origin.

III. INTENSITY.

Under gradation of intensity of stimulation the scratch-reflex markedly exhibits correspondent grading of intensity of motor response. This is traceable more easily with electrical excitation than with mechanical, gradation of the former being more easily manageable than of the latter. With induced currents as stimuli the bringing of the secondary coil step by step nearer the primary suffices to give a dozen or more successive degrees of intensity of the reflex from a single skin point without any shift of the stigmatic exciting electrode or any alteration in the interrupting key in the primary circuit. The increase in intensity of the reflex shows itself in increase of the amplitude of beat of the movement with usually little or no acceleration of the rhythm. This is so whether the rate of frequency of the exciting stimuli be rapid or not, so long as it lies above the necessary minimum mentioned above. The increase in the amplitude of the beat may be very great. I have one graphic record in which the excursion under the intenser stimulus is thirteen times as great as under the weaker stimulus. Fig. 10 exhibits six grades of the reflex from a series of twelve obtained in succession at one minute intervals by successively bringing the secondary coil nearer the primary, and thus progressing from weaker reactions to stronger in order to exclude possible simulation

¹ Sherrington, *Proc. Physiol. Soc.* p. xvii, 1904; this *Journ.* xxxi.

² *Archives internat. de Physiol.* i. i, 1904; *Onderz. g. in het Physiol. Labor.*, Utrecht, v. 2, 1905.

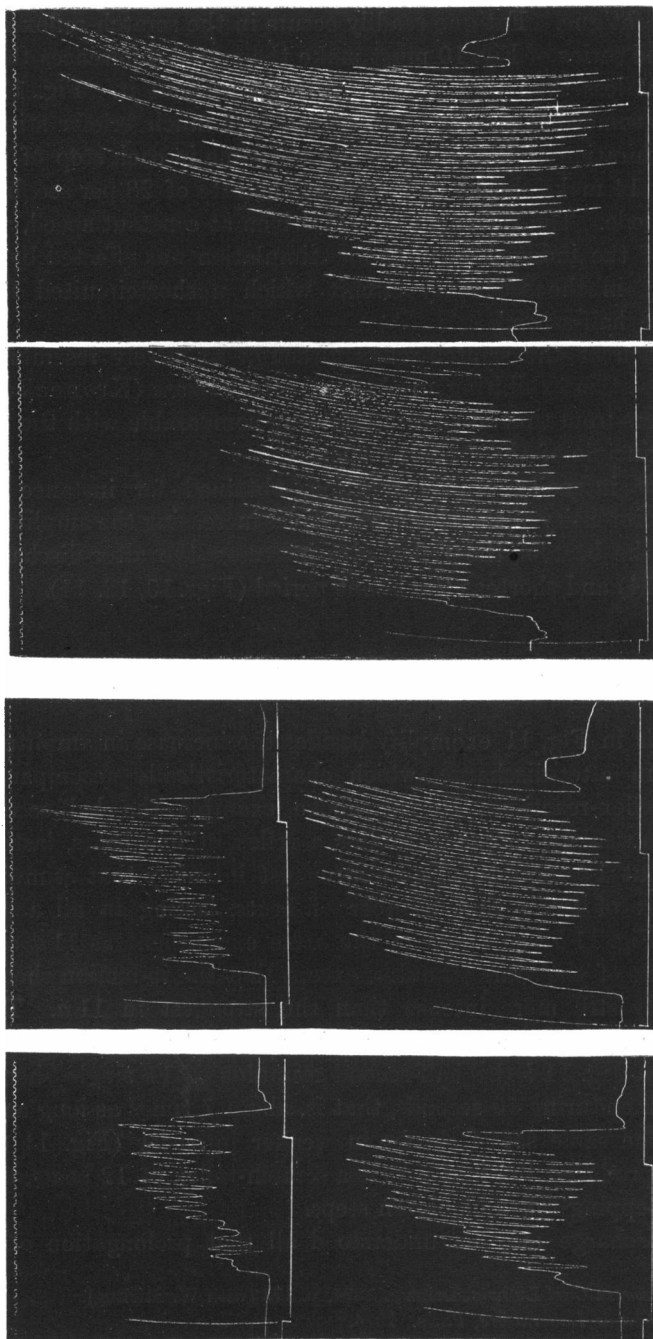


Fig. 10. Scratch-reflexes excited from some skin point at successive intervals of one minute, and excited by unipolar faradisation with shocks unaltered in rate, etc., but of intensity increasing in regular steps from tracing 1 to 6 inclusive. The signal below. Time above in $\frac{1}{4}$ th secs.

of grading by fatigue. Fatigue readily occurs in the scratch-reflex and its effect in the series of Fig. 10 must make the actual differences there seen somewhat less than they would really be without it. Fig. 11 *a* shows a series somewhat similar but obtained by a much briefer stimulation. The duration of the stimulus was the same in each step of the series, namely 14 make shocks delivered at the rate of 28 per sec. by a stigmatic kathode. The rotating key was driven at constant speed, and the delivery of the induced currents for stimulation was effected by an automatic key in the secondary circuit which unshortcircuited that circuit for one half-second.

The reaction of the scratch-reflex although so closely resembling that of the heart in exhibiting marked refractory phase (Kronecker¹, Marey²), differs from that in showing nothing comparable with the 'all or nothing' principle of the cardiac response.

Increase of intensity of the reaction, obtained for instance by increasing the intensity of the stimulus, besides increasing the amplitude and force of the beat of the reflex also increases the after-discharge (Figs. 11, 12, 14) and shortens the latent period (Figs. 10, 12, 14).

IV. AFTER-DISCHARGE.

The records in Fig. 11 exemplify besides the increase in amplitude the increase in after-discharge, which characteristically accompanies intensity of reflex-reaction. In the above example the half-second stimulus in its weakest intensity excites a reflex of five beats, lasting altogether about 1.5 seconds. In its strongest intensity that stimulus excites a reflex of twice that number of beats, lasting in all about 3.5 seconds. Fig. 11 *b* was taken in the same experiment as 11 *a* and shows the result of the same stimulus, except that the induction shocks are individually still more intense than the strongest in 11 *a*. The translation of the recording surface was however reduced to condense the record. In Fig. 11 *b* the half-second stimulus of 14 single shocks excites a reflex enduring 10 seconds, that is, about 7 times as long as is produced by the same set of shocks in weaker intensity (Fig. 11 *a*). Of the reflex produced the first part is a scratch-reflex of 12 beats, the latter part a stepping-reflex of eleven steps.

By after-discharge may be understood all that prolongation of a

¹ *Festgabe zu Carl Ludwig*, Leipzig, 1874, p. 173 (with W. Stirling).

² *Travaux de Laboratoire*, Paris. 1876.

reflex which ensues subsequent to cessation of the application of the exciting external stimulus. No feature of reflex reaction distinguishes it from nerve-trunk or nerve-tract conduction more fundamentally than lengthy after-discharge. Though marked in the scratch-reflex, it is in that reflex not so extensive, in my experience, as under comparable degrees of excitation in some other reflexes, *e.g.* the flexion-reflex of the hind limb, the crossed extension-reflex of the hind limb. In the scratch-reflex the after-discharge is rhythmic and clonic like the rest of the reflex. With stimuli of moderate length and intensity it is usual for the after-discharge to have an extent of 3—4 beats. With quite brief

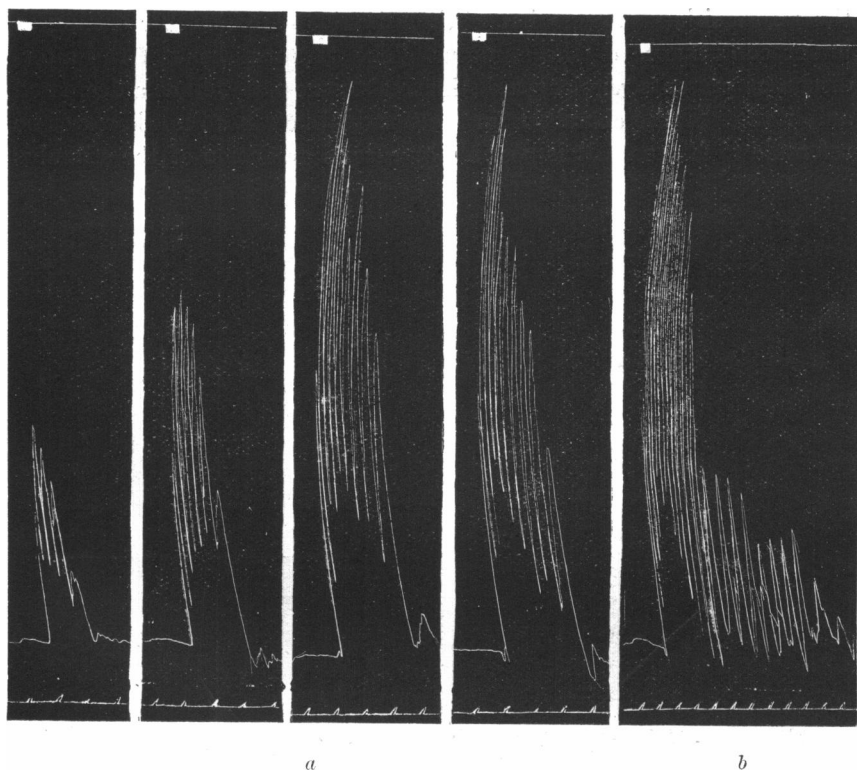


Fig. 11 *a, b.* A series of scratch-reflexes excited by unipolar delivery of the same number of break shocks at the same frequency but of increasing intensity. Time in secs. The number and duration of the series of induction shocks is recorded above. In the tracing (*b*), the furthest to the right, the speed of travel of the recording surface was reduced from what it had been in the tracings furnishing (*a*); otherwise the record remained unaltered from (*a*). In (*b*) the stepping reflex ensues as the end of the after-discharge of the reflex.

stimulations the whole stimulation may fall within the latent period of the reflex and so the whole visible reflex appear as after-discharge (Fig. 12 *c*). Such an occurrence emphasises the feature that the rhythm of the response is independent of rhythm in the external stimulus. If an external stimulus of nine oscillations delivered at 20 per. sec. rhythm evokes after its own cessation a response in one case of ten oscillations at 5 per sec. and in another case a response of two oscillations at 3 per sec. there can hardly, although both stimulus and response are rhythmic, be any close relation between the rhythm of the one and the other.

The beats of the after-discharge of this reflex exhibit the slight lengthening of duration and sequence characteristic of the ending of the reflex either on cessation of the stimulus or on fatigue setting in under continuance of the stimulus. The terminal beat of the after-discharge presents regularly a distinctive slowness as well as a decreased amplitude. These characters in the terminal beat need not however be referable to fatigue. It is possible by careful gradation of the stimulus

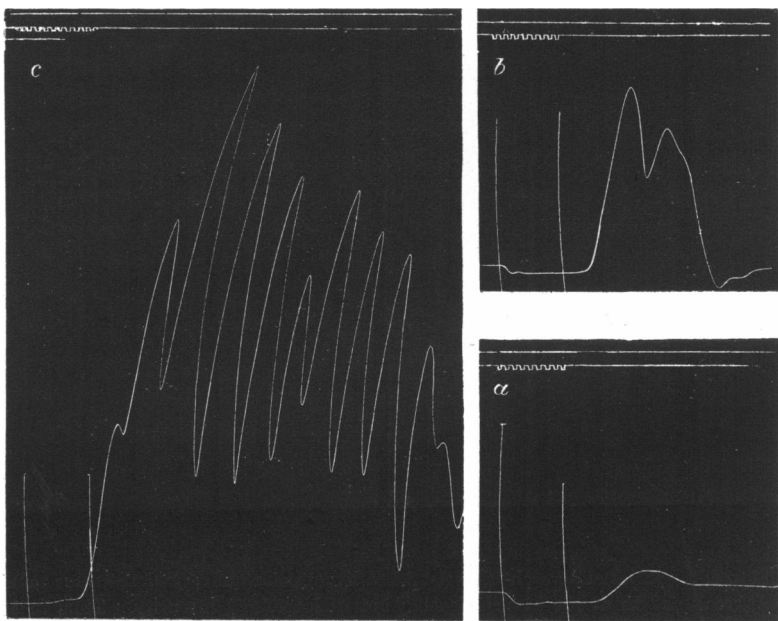


Fig. 12 *a, b, c*. Three scratch-reflexes evoked by the same series of make shocks delivered unipolarly to the same skin spot, but with the intensity of the shocks greater in *b* than in *a*, in *c* than in *b*. In *a* the reflex gives only one single beat; in *b* it gives two beats; in *c* ten beats. The exciting make shocks are recorded above.

toward threshold value to evoke a scratch-reflex of one beat only (Fig. 12 *a*). That single beat resembles in duration and amplitude the ordinary terminal beat of the after-discharge. The slow and feeble character of the beat as the ordinary reflex dies away after excitation is therefore not a sign of fatigue necessarily, but indicates weak excitation relatively to capacity for response at the time. It shows that though the external stimulus may cease abruptly the internal excitation and the reaction of the reflex-arc itself subside gradually. This forms another item of evidence that the rate of rhythm of the reflex although it can be stated broadly to be independent of external conditions of excitation is strictly speaking not wholly so. The weaker stimulus results in a slightly slower rate; or, more generally expressed, the weaker reaction exhibits a slightly slower rate.

V. SUMMATION.

One single induction shock never in my experience suffices to evoke the scratch-reflex. In this the reflex resembles the reflexes from the hind limb of the frog as examined by Stirling¹ in his well-known research. For the scratch-reflex a single induction shock remains a subliminal stimulus, even when sufficiently intense to cause on its application a general movement of the whole animal. But induced currents serially delivered easily excite the reflex even when feeble in intensity, often when imperceptible to the tongue. The reflex can not unfrequently be evoked by two strong single (or double) shocks. I have a record where two break shocks delivered '22 sec. apart excited a scratch-reflex lasting nearly two seconds and exhibiting nine beats. As to the time interval from stimulus to stimulus across which summation can take effect I find it longer with strong stimuli than with weak. The reflex can be excited by double shocks succeeding each other even so slowly as one double shock in 1·6 sec. That is the slowest frequency at which I have observed summation. At frequencies above once per sec. summation occurs more effectively and with lower intensities for the individual stimuli. At the frequency of stimulus supplied by the dog's foot itself in scratching the receptive skin field, namely at about 4·8 stimuli per sec., the summation is very facile.

Summation in this reflex is well shown in the relatively long times and series of stimulation which, after extended latent delay, do yet

¹ Ludwig's *Arbeiten*, Leipzig, p. 372. 1874.

ultimately succeed in provoking the reflex (Fig. 13). My records include instances where the reflex breaks out after 46 make shocks delivered at 18·2 per sec. and where it breaks out after 42 double shocks

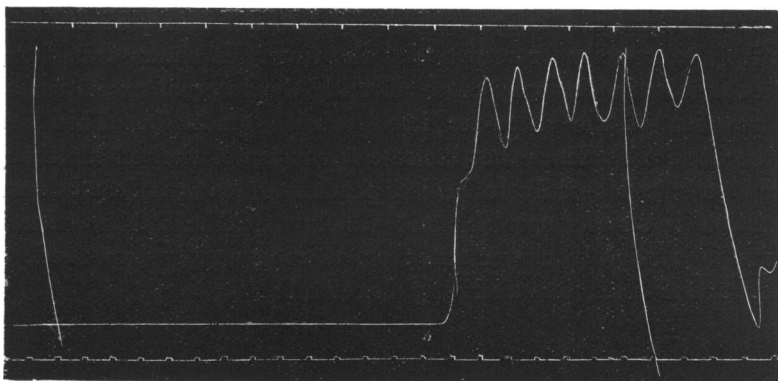


Fig. 13. Scratch-reflex evoked by summation of rather weak double shocks, unipolarly delivered at the moments recorded on the top line. Time below in $\frac{1}{4}$ th sec.

delivered at the rate of 12·5 per sec. The latent period in these cases extends to more than 2 and 3 seconds respectively, although under stimulation of quicker rate the latency is usually little more than ·15 sec. The shortest latency in my records measures ·085 sec. The intensity of the individual shocks remaining the same, the less their frequency (beyond a certain minimal interval), the longer the series required to reach efficiency by summation. The internal influence exerted as latent effect by the stimulus therefore fades gradually out, and as said above traces of it are discoverable even 1·6 sec. after lapse of a momentary external stimulus if that stimulus has been, though brief, intense. As demonstrated on the frog by Stirling¹ the rate of the stimuli (induction shocks) applied to the skin remaining the same, the period across which they will sum to excite the reflex reaction varies inversely as their intensity. Fig. 14 shows four scratch-reflexes, excited each by 43 make shocks delivered at the rate of 40 per sec., the same speed of rotation of the interrupting key being maintained throughout the series of reflexes. Drawing the secondary coil nearer the primary and thus increasing the intensity of the induced currents from 690 to 1100, 1900, and 5000 units of the Kronecker scale respectively decreases the latent period. At 1100 units it is ·88 sec., and at 5000 units it is ·45 sec.

¹ Ludwig's *Arbeiten*, Leipzig, *loc. cit.* 1874.

One result of this is that with the weak stimulus scarcely more than one beat of the reflex response falls within the period of the brief stimulation employed. The example also shows the increase of after-discharge with increase of intensity of reaction, and the little influence which intensity has on the rate of rhythm of the reflex. There should

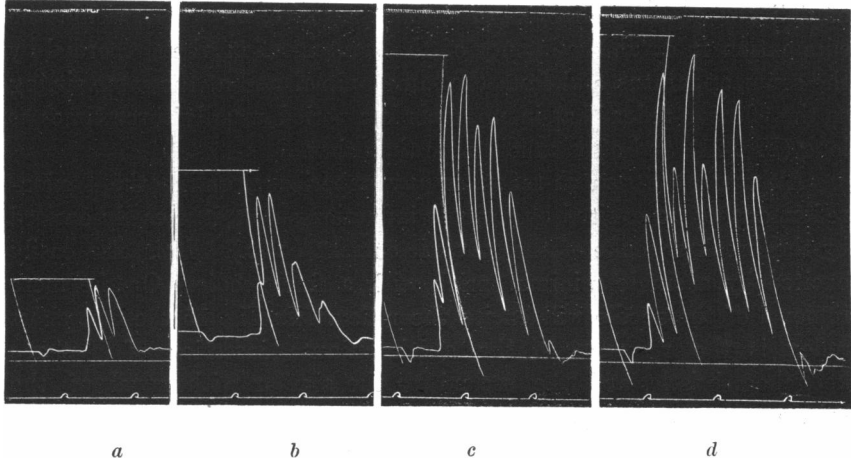


Fig. 14 *a, b, c, d.* Series of scratch-reflexes evoked by the succession of break shocks (top line). Time below in sec.

be some relation between the length of after-discharge and the length of interval across which summation between stimulus and stimulus should occur. In consonance with that supposition it is found the after-discharge and the summation interval both of them last longer with stronger stimuli than with weaker. But the length of after-discharge visible in the records of the reflex-response is greater with strong stimuli (*e.g.* Fig. 11) than the longest summation interval I have obtained, although the reverse is what might have been expected. I do not think instrumental inertia in my observations explains this difference. It would rather seem that the length of after-discharge evidences a cumulative internal effect, and by using gradually increasing intervals between the successive stimuli employed for examining summation interval in the later period of a reflex a summation interval might be found more closely agreeing in length with the length of after-discharge.

The latent period of the scratch-reflex is in my experience habitually longer than that of various other reflexes in the 'spinal' dog's hind-limb, notably than the homonymous flexion-reflex and the 'extensor-thrust.' The latent period varies much according to conditioning circumstances,

even in one and the same type reflex. In spite of such variation repeated experience with the reflexes soon makes the observer aware of an unmistakably greater average latent delay with the scratch-reflex than with the other reflexes above mentioned. Taking instances where the intensity of external stimulus for both has been approximately the same and of fairly high strength, and exactly alike in regard to the rate of delivery of the individual stimuli of a series, and well within the summation interval, the latency of the scratch-reflex when recorded by the same apparatus and from the same animal and at the same sitting as the 'flexion-reflex' has in my records a period usually three times as long (Fig. 21), and often much more than that.

Although the scratch-reflex, in my experience, unlike the flexion-reflex, cannot be excited by a single induction shock, it is easily excited by the break or make of the galvanic current (*v.s.p.*). It is also easily excited by a single minimal prick with a fine needle. Or the mere removal of the needle will excite the reflex. In Fig. 15 the first short reflex is the response to the quick minute insertion of a sharp hedgehog bristle, and the second to the similar withdrawal of the bristle.

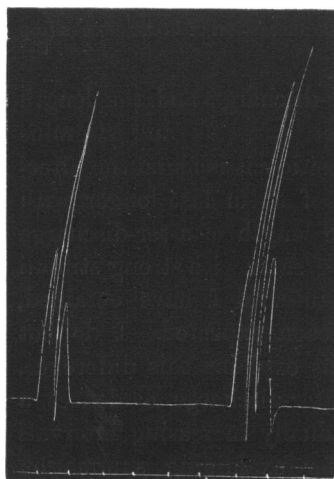


Fig. 15.

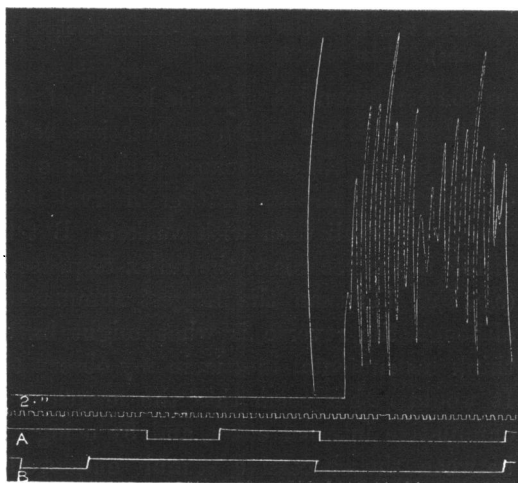


Fig. 16.

Fig. 15. Scratch-reflexes evoked at the moment of insertion into and of withdrawal from the skin of the point of a sharp hedgehog spine.

Fig. 16. Summation effect by stimulating subliminally two points 9 cent. apart in the receptive field. *A* signals the stimulation at one point, *B* that at the other. Time in fifths of seconds.

VI. IMMEDIATE SPINAL INDUCTION.

In the summation described above a pre-current stimulus delivered at a skin point exerts in the reflex-arc a facilitating influence ('*bahnung*,' Exner) for a stimulus ensuing at the same point within an interval sometimes as long as 1600 σ . From general knowledge of the reactions of the peripheral nerve trunks and the skeletal muscles concerned in the reflex it seems permissible to exclude these structures as the seat of the *bahnung*. But the phenomenon might be referable to the cutaneous receptive organs whose excitation provokes the reflex, or might be referable to the central nervous mechanisms of the reflex-arc. From collateral evidence obtained by Exner and many others in other cases of *bahnung* the latter seat seems the more probable, and experiment is able to fairly conclusively show that it is so in the scratch-reflex.

At a point *A* in the receptive skin field there is applied a series of induction shocks of such intensity and at such rate as to be subliminal in excitatory value, but not far below the threshold. At another point *B* in the receptive skin, distant for instance 9 cent. from *A*, a similar subliminal series is applied. Though the two stimulations applied separately are each subliminal, on being applied together they are supraliminal and excite the reflex (Fig. 16). The reason of this might be that the current applied at either stigmatic electrode, *e.g.* at *A* extended in physical distribution so as to overlap in the skin the current applied at the other stigmatic pole, *e.g.* at *B* sufficiently to raise the physical value of the stimulus above the threshold, although the intensity of the currents used is very feeble. Against such an explanation is the circumstance that the effect is still obtainable when the stigmatic electrodes are even 20 cent. apart (Fig. 17 *a*). And the effect is cut out by a local injection of cocain into the skin at one of the two places of stigmatic excitation. Further, the effect is obtainable with induction shocks so delivered that they fall alternately at *A* and *B*. The combined effect therefore appears not explicable by physical overlapping of the two stimulations. It seems that just as the effect of a subliminal stimulus favours the effect of a stimulus subsequently delivered at the same skin point, so also it favours the effect of stimuli delivered at circumjacent skin points. There seems therefore a *bahnung* in which subliminal stimulation of a reflex-arc *A* reinforces stimulation of another and adjacent arc *B*.

This result might obviously in the present case be explicable in either of two ways. It might be that when the skin point *A* is stimulated a particular group of the efferent neurones innervating the muscles employed by the reflex is thrown into action, and similarly another group when skin point *B* is stimulated. The reflex movement

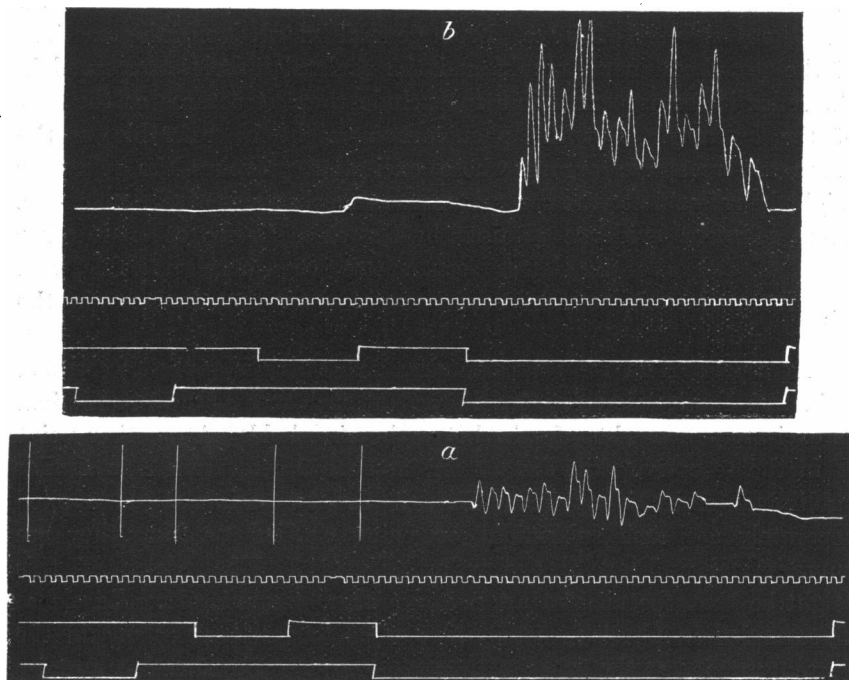


Fig. 17 *a, b.* *a*, same as Fig. 16 but with skin points 20 cent. apart. *b*, same but with skin points 15 cent. apart.

which appears when points *A* and *B* are both stimulated at the same time might then be due to mechanical summation of two contractions each of which is of itself alone too slight to cause perceptible movement. In other words, the reinforcement would be due not to response in the motor neurones being more intense in any one of them, but to the number of motor neurones in action under the combined double excitation being double what it is under excitation of the two skin points taken singly. On the other hand, the reinforcement might be due to the group of motor neurones upon which the reflex-arc starting at skin point *A* impinges, being more or less common to the reflex-arc starting at skin point *B*. The reflex resulting under combined

stimulation of the two skin points would then be due to greater intensity of excitation of the same individual motor neurones.

The dilemma is therefore between extensity and intensity. Importance attaches to its solution, because in the former explanation it would not follow that the arcs had any mechanism in common, whereas on the latter explanation there must be a constituent mechanism common to the sets of arcs arising at both of the separate skin points *A* and *B* respectively. But the reflex elicited by the conjoint stimulation has a rhythm which as compared with that of the reflex elicited by stimulation applied at either of the separate points shows no trace of reduplication. There is no evidence of two rhythms in the resultant end-effect. Here as in the previously mentioned summation the refractory phases in the reflex produced at *A* or *B* apply also in the combined reflex. This implies that the afferent arcs *A* and *B* impinge actually upon a common mechanism, and that the motor neurones involved are common to both of the two arcs arising at *A* and *B* respectively. The same conclusion is led to by another form of the experiment. To become effective by summation the individual stimuli, *e.g.* break shocks applied at a skin point, must follow each other at intervals of time not too prolonged, the interval being *ceteris paribus* shorter the less intense the individual stimuli. When induction shocks are applied at *A* at such frequency, *e.g.* twice a second, that at the intensity chosen they fail, on account of the slowness of their recurrence to evoke the reflex, if a similar series of induction shocks be applied at *B* similarly unable to evoke the reflex, on applying the two series of stimuli concurrently in such a manner that each stimulus at *B* is delivered about midway in the interval elapsing between the successive stimuli at *A*, the reflex is evoked.

These results indicate that the reinforcement in the central mechanism is in the nature of a reinforcement of intensity rather than of extensity. It argues that the reflex-arcs from the separate skin points *A* and *B* do in fact act upon the same motor neurones. The spread of *bahnung* from reflex arcs arising at *A* to central apparatus also shared by arcs arising at *B* may be obtained when skin points *A* and *B* are taken practically anywhere in the receptive field at not too great a distance apart. The reinforcement, is, however, greater when the points taken lie nearer together than when they lie farther apart. The greatest interval between the points at which I have been able to obtain distinct reinforcement is 20 cent. With skin points nearer together than 3 cent. the reinforcement is very marked indeed, but at

that distance there is more likelihood of physical overlap of the two stimulations.

The fact that the reinforcement becomes more marked as the distance between the points of separate stimulation decreases (Figs. 16, 17*a*, and 17*b*) suggests its explanation by overlap of the physical stimuli. Objections to that explanation have been mentioned above. Another explanation of the increase soon suggests itself to the observer. The scratch-reflex in the spinal dog carries the foot approximately toward the place of excitation. When the irritation lies far forward in the receptive skin-field the foot is carried further forward, and when the irritation lies high dorsally the foot is carried further dorsally, and when the irritation lies far back the foot is not carried so far forward. A scratch-reflex excited from far back and high up in the field is therefore not wholly like a scratch-reflex evoked from far forward and low down. These differences

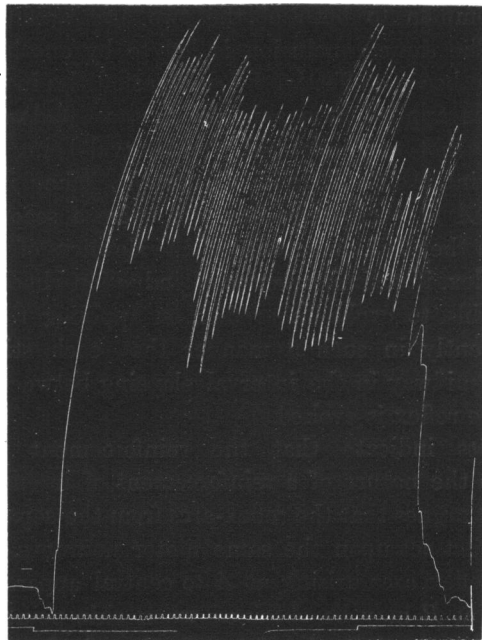


Fig. 18. Scratch-reflex. The 'high' form of the reflex. Signal below. Time in $\frac{1}{8}$ th secs.

are easily registered in graphic tracings. Fig. 18 shows the form of the reflex when the skin point excited lies far back and high dorsally; it may be compared with Fig. 2, where the skin point was far forward and

low. The nearer together two points are in the receptive field the closer the likeness between the scratch-reflexes that they initiate. In other words, the stronger mutual reinforcement found to obtain between two skin points near together as compared with the mutual reinforcement between points far apart is consonant with the greater likeness between the two reflexes excited by them. Or again, in other words, the alliance between the reflexes is greater the greater the likeness between them.

This form of '*bahnung*' of one reflex by another resembles certain of the visual reactions termed by Hering 'induction' so closely that 'spinal induction' seems a useful designation for it. But it differs probably fundamentally from another form of '*bahnung*' which I have described elsewhere¹ and to which the term 'spinal induction' in like manner is applicable. That other form of 'spinal induction' appears to occur as a rebound in succession to inhibition and I have termed it therefore 'successive spinal induction.' The form of 'spinal induction' described in the present section seems to set in at once as a primary effect of, and not a rebound from, the applied excitation. It may for that reason be termed '*immediate spinal induction*.'

VII. THE RECEPTIVE FIELD.

The whole area of skin from whose points the scratch-reflex can be elicited may be conveniently termed the *receptive field* of that reflex (Fig. 19). The receptive field may be considered as composed of receptive points. That is to say, what is referred to as 'the scratch-reflex' in general is strictly speaking a group of reflexes all more or less alike, all using broadly speaking the same motor apparatus in broadly speaking the same way. And this group of individual reflexes forms a physiological group not only on account of their general similarity but also because they act harmoniously upon the same efferent path, and, in many instances at least, demonstrably reinforce each the other's action on that efferent path. Their intraspinal mechanisms are to a large extent knit together into an unitary whole. The scratch-reflex as a whole may therefore be referred to as a 'type-reflex.' The kind of harmonious and reinforcing relationship between the individual reflexes comprised in the 'type-reflex' may be indicated by terming them 'allied reflexes' and their arcs 'allied arcs².'

¹ *Proc. Roy. Soc.*, Feb. 1905 B. 76, p. 159.

² *British Assoc. Reports*, Address to Section I, Cambridge. 1904.

Similarly with various other reflexes. In the limb the 'flexion-reflex' and the 'crossed extension-reflex' are each of them 'type-reflexes.' Each is a group of reflexes. The individual reflexes comprised in each of these 'type-reflexes' have such mutual relationship among themselves that they act harmoniously together upon the motor neurones of the type-reflex, and these motor neurones are practically common to them all. The motor neurone may in the relation which it thus holds to a number of reflexes in common be usefully designated the 'final common path.' The individual reflexes comprised in a type-reflex are allied reflexes because the mutual relation between their action on the final common path is one of harmonious alliance, and not of inhibition or interference.

The extent of the receptive field of a type-reflex is often wide. It is much wider in some type-reflexes than in others; thus, that of the flexion-reflex of the hind-limb (cat, dog) is more extensive than that of the extensor-thrust of the same limb. The former includes the whole skin surface of the limb below the knee and a large part of that of the thigh. The receptive field of the extensor-thrust seems practically confined to the plantar surface of the foot. The receptive field of the scratch-reflex as revealed by spinal transection in the posterior cervical region is indicated in Fig. 19. It is really more extensive, for it includes some at least of the side and back of the neck; this latter portion can be revealed by spinal semisection in the anterior cervical region. In my experience the receptive field of this reflex is not always a perfectly continuous area. The main dorsal saddle-shaped area may not actually meet outlying parts of the field in which certain of the nipples lie. Within the receptive fields of the type-reflexes not all the receptive points serve with equal facility or potency to excite the reflex. The points composing certain areas of the field are most effective, those of certain other areas least effective, and from the rest of the field the reflex is elicitable with intermediate degree of ease. The area whence the reflex can be evoked with least facility forms usually a circumferential zone. The area where the threshold value of stimulus is lowest lies usually fairly remote, though not equally remote, from all the borders of the field. The reflex effect of a weak stimulus in this central focal area seems to resemble the effect of a stronger applied in the border zone. Reflexes of an intensity unobtainable from the border zone are easily provokable from the focal area. In the flexion-reflex of the dog's hind-limb the toes and plantar cushion lie in the focal area. In the scratch-reflex of the dog the focal area extends along that part of the

field adjoining the mid dorsal line, especially at and near behind the scapular region; in Fig. 19 from 5 to 15 in the horizontal row of numbers and from the mid-line laterally to 8 in the vertical row. The difference between the threshold values of stimulus for the focal and border zones may be very considerable.

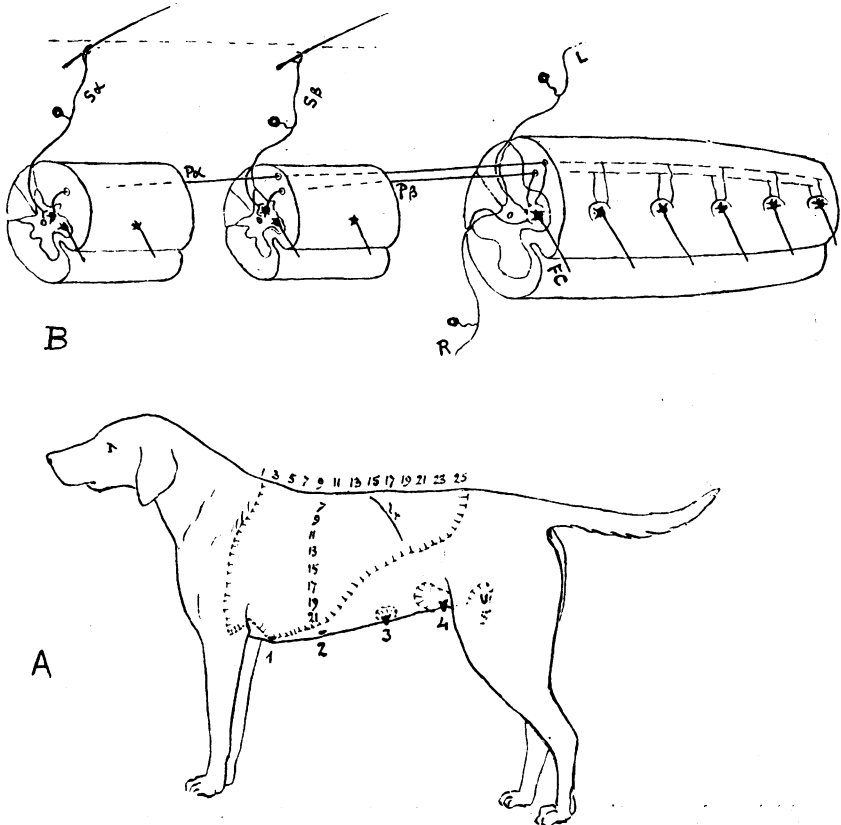


Fig. 19. The Scratch-Reflex.

- A.—The 'receptive field,' as revealed after low cervical transection, a saddle-shaped area of dorsal skin, whence the scratch-reflex of the left hind-limb can be evoked. *lr* marks the position of the last rib.
- B.—Diagram of the spinal arcs involved. *L*, receptive or afferent nerve-path from the left foot; *R*, receptive nerve-path from the opposite foot; *Sα*, *Sβ*, receptive nerve-paths from hairs in the dorsal skin of the left side; *FC*, the final common path, in this case the motor neurone to a flexor muscle of the hip; *Pα*, *Pβ*, proprio-spinal neurones.

When electrical stimuli are employed the following are instances of the differences found between the values of threshold stimuli at various points in the receptive field of

the scratch-reflex of the spinal dog in the same animal and at the same sitting. The situation of the points in the field is indicated by fractions, a number from the longitudinal row in Fig. 19 being numerator, a number from the vertical row denominator. Double induction shocks at a rate of 25 per sec. were used throughout and delivered unipolarly by an entomological pin-point lightly inserted. The intensity of the stimulus is expressed in the units of the Kronecker inductorium scale.

Place of excitation	Threshold value of physical stimulus
$\frac{5}{15}$	420 units
$\frac{2}{14}$	360 "
$\frac{3}{18}$	no reflex even with 10,000 "
though the reflex could be fairly easily excited from this spot by mechanical stimulation, <i>e.g.</i> , rubbing with a pencil point.	
$\frac{13}{13}$	190 "
$\frac{8}{13}$	90 "
$\frac{3}{13}$	50 "
$\frac{13}{8}$	140 "
$\frac{8}{8}$	50 "
$\frac{3}{8}$	140 "
$\frac{23}{4}$	220 "
$\frac{13}{4}$	120 "
$\frac{11}{4}$	80 "
$\frac{8}{4}$	15 "
$\frac{5}{4}$	40 "
$\frac{3}{4}$	50 "

Expressed in this way the threshold value of stimulus at some points of the field is more than twenty-five times as high as at others.

Although the absolute value of the threshold may vary much in one and the same animal at different times, *e.g.* from day to day, the relative values vary less. But this relative value is upset by 'local fatigue,' etc. With variations in the general excitability of a type-reflex from time to time the size of the receptive-field varies, the field expanding when the excitability is high and contracting when it is low. During 'spinal shock' the reflex may therefore if elicitable at all be elicitable only from the focal area. The receptive-field of the scratch-reflex usually exhibits besides its main focal area subsidiary ones, *e.g.* at certain nipples.

The coalescence of the allied reflexes embraced in one type-reflex tends to make weak stimuli applied to a larger area of the receptive field equivalent to intenser stimuli applied to a smaller area, and to make stimuli applied to a larger area in the extra-focal region of the field equivalent to stimuli applied to a smaller area in the focal region. A stimulus applied at point *A* in the field exerts *bahnung* and reinforcement for stimuli at circumjacent points *B*, *C*, etc., not only when the latter happen synchronously with it but also when they happen subsequently to it. But the time-interval across which summation can occur is less prolonged than when the subsequent stimulus falls at *A* itself. The intraspinal effect produced by a stimulus at *A* though it irradiates about the central end of the arc belonging to *A* is not so intense or prolonged elsewhere as at the central end of the arc of *A* itself. Thus at the central end of the arc of *A* itself the effect may remain detectable as stated above for 1600 σ , but it is not so long detectable at the parts of the intraspinal mechanism upon which the central ends of the arcs of *B*, *C*, etc. impinge, and its persistence seems less in rough proportion to the degree in which points *B*, *C*, etc. lie distant from point *A*. Therefore in spite of the before-mentioned evidence that the reflex arcs from separate areas of the receptive field are closely knit together intraspinally, the reflex arcs arising in separate parts of the field seem nevertheless to possess each their own more or less separable focus of action in the intraspinal mechanism of the reflex. The nervous mechanism of the scratch-reflex bears in this, as in so many other respects, striking analogy to that of the nervous system of medusa as exhibited in the reactions of the swimming-bell (Romanes, Nagel, Bethe, and others).

With punctiform stimuli of feeble intensity applied to the peripheral region of the retina it is found that movement of the image increases its visibility. A somewhat similar result is met with mechanical stimuli applied to the receptive field of the scratch-reflex. A touch that hardly excites the reflex or just fails to excite it will if repeated with a certain time-interval at points a centimetre or more apart from each other succeed in exciting it quite briskly. The observations can be made by lightly running a spur wheel along the receptive field. It succeeds even when the tips of the spokes lie as far apart as 2.5 cent. Here the immediate spinal induction described above for electrical stimuli is evidently answerable for the summation.

An observation of somewhat similar kind is the following. A linear stimulus, for instance the edge of a card 20 cent. long, applied to the

skin of the receptive field is not nearly so provocative of the reflex if applied simultaneously along its whole length and kept in steady apposition to the skin, as it is if applied by running one corner of it along the skin for the 20 cent. distance, and in the same time *e.g.* 10 secs. as the whole card edge was applied. In the former case a slight reflex may be excited at outset and with even less likelihood at removal of the linear stimulus but there is no reflex during the constant application of the card. In the latter a reflex is excited soon after the stimulus begins, and becomes brisk and is continued throughout the whole period of application. It is a difference between a simultaneous line and a moving point and the latter is much the more effective stimulus for the scratch-reflex.

The after-discharge of a reflex following cessation of the physical stimulus closely resembles the positive after-image resulting from a visual stimulus. Its relation to the intensity of the reaction which it concludes, its undulatory character both in the scratch-reflex and also in the steadily tetanic flexion-reflex, offer analogy to features of the visual after-image. Immediate spinal induction extending from the central apparatus of one receptive area to that of others seems to have an analogue in visual irradiation.

VIII. FATIGUE.

When a stimulus is sustainedly applied to the receptive skin the scratch-reflex movement excited soon shows signs of waning. This occurs both with mechanical and with electrical stimulation, but earlier with the latter. It might be that with electrical stimuli the waning intensity of the reflex arose from weakening of the stimulus by polarisation at the electrodes. Polarisation soon occurs there, but a similar though not so rapid decrement is seen in the reflex under mechanical stimulation. The beat becomes less ample and the rate of beat less frequent. The decline is greater than occurs usually under mere weakening of a stimulus that is still supra-liminal. Further, the rhythm becomes not only slow but irregular and the beats become very irregular in amplitude. Finally, under continued stimulation the reflex-response dies quite away, to give however brief reappearances in imperfect groups from time to time if the stimulus be still in spite of the decadence of the reflex-response continued further still. This waning of the reflex seems referable to a form of that kind of process which is usually in physiology termed 'fatigue.'

Under this 'fatigue' the frequency of the rhythmic movement may sink from 5 beats per sec. to 3 per sec. or even 1·5 per sec. (Fig. 20; mechanical stimulation) before the reflex-response actually disappears. In this condition of the reflex a strong stimulus is required to excite, and the reflex even under the strongest stimulus may be slow and irregular with long initial latency and poor brief-lasting 'after-discharge.'

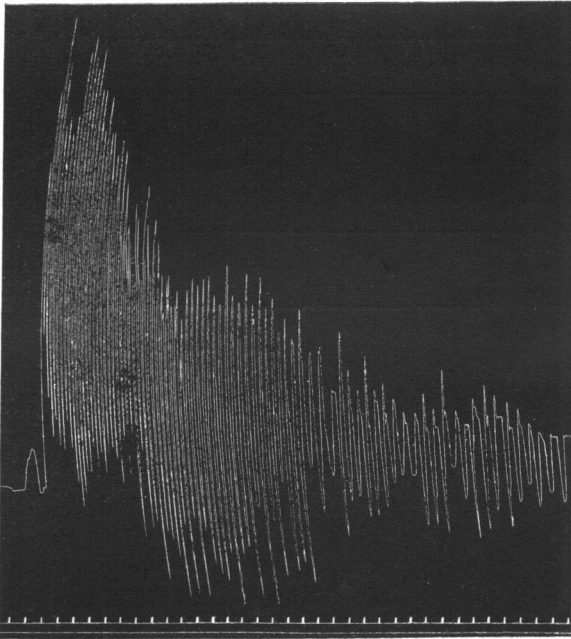


Fig. 20. The scratch-reflex showing alteration of reflex under prolonged mechanical stimulation of a single spot of the receptive field. Time in secs.

'Fatigue' in my experience ensues more quickly in the scratch-reflex than in the flexion-reflex. Fig. 21 shows the duration of the scratch-reflex and of the flexion-reflex in the same dog in the same five minutes, and obtained by unipolar faradisation (break shocks) at the same frequency, and with the secondary coil at the same distance from the primary coil for both reactions. The scratch-reflex dies out after 8 secs., exhibiting some slow concluding beats before lapsing altogether. The flexion-reflex on the other hand is after 12 secs. duration still unappreciably affected by fatigue: at the 10th second it has in fact shown an increase in the response, which it very often does exhibit about that time, due to increase of flexion action at the hip. It is

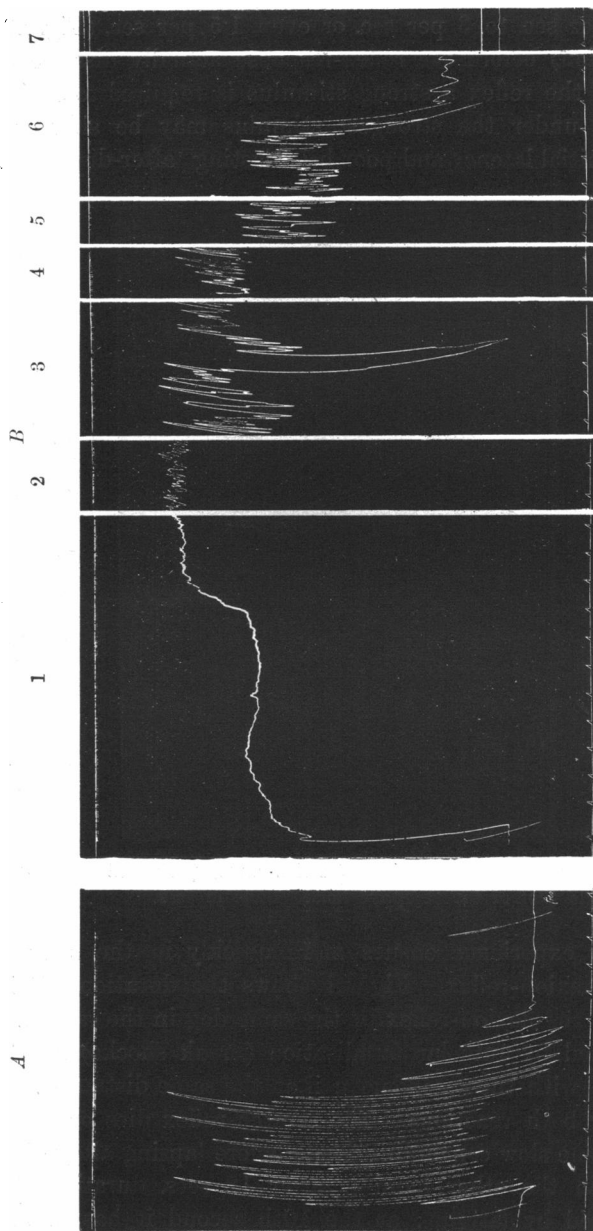


Fig. 21. Contrast between the scratch-reflex *A* and the flexion-reflex *B* under the same stimulus. The top line shows the delivery of the induced currents used for the stimulation at the same rate for both reflexes. Time below in secs. In *A* the stimulus was discontinued after the 11th second, the reflex having completely given out. In *B* the stimulus was continued for 95 secs. and there was still at the end of that time considerable reflex response. The portions of the reflex shown in 2, 3, 4, 5 and 6 correspond respectively with the 18th, 42nd, 52nd, 72nd and 92nd seconds. The phase in 3 is explicable by 'successive spinal induction.' The reduction of the figure does not allow the record of exciting shocks (top line) to be legible.

difficult under unipolar faradisation to maintain a scratch-reflex for more than 45 secs. On the other hand, I have by similar excitation seen the flexion-reflex maintained for 15 minutes, although of course showing signs of fatigue. Both the scratch-reflex and the flexion-reflex recover from such 'local' fatigue with remarkable rapidity (Fig. 22). Repose of 15 secs, or even as little as 10 secs, often suffices to temporarily remove in large measure the characters of fatigue from the reflex reaction of these arcs. Fig. 22 shows the latter part (39 secs.)

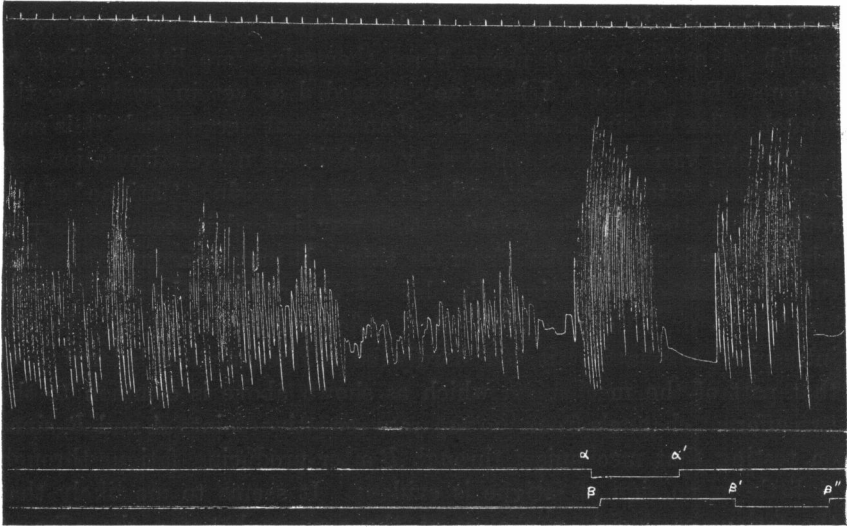


Fig. 22. The scratch-reflex under 'local fatigue.' Lowest line marks application and reapplication of the mechanical stimulation at the skin point yielding the fatigue effect. Signal $\alpha - \alpha'$, marks the time of application of a similar mechanical stimulus to a neighbouring skin point. Time above in secs.

of a prolonged scratch-reflex induced by mechanical stimulation. The lower signal line B indicates by its depression the time of application of the stimulus that is producing the 'fatigue.' The line is depressed at commencement (left-hand side) of the figure, because the stimulus has already been in operation for 40 secs. The reflex elicited is seen to be almost tired out by the moment marked β by the B signal. The stimulus was then discontinued and on recommencing at β' , 10 secs. later, the reflex is seen to have notably recovered from the fatigue as shown by the tracing corresponding with the time $\beta' - \beta''$. The upper signal line A marks the time of application of another mechanical stimulus to another area of receptive skin field only two centimetres

from the one at which fatigue was induced. The reflex α — α' from the second area shows but little sign of the fatigue induced in the reflex from the other area excited immediately prior to itself.

This fatigue may be described as 'local' because when the reflex excited from one small area *A* of the receptive skin has developed the fatigue-change, reflexes evoked from points *B*, *C*, &c. circumjacent to *A* show little participation in the fatigue-change induced from *A*. I have noted a similar result with other reflexes¹. It would indicate either that the local nerve-ending in the skin, or that the intraspinal mechanism itself, is the seat of the fatigue-process, since there is wealth of evidence that nerve fibres themselves are little subject to fatigue. But although I have not succeeded as yet in producing the scratch-reflex by direct stimulation of an afferent nerve-trunk, it is easy to provoke various other reflexes by such direct nerve stimulation, *e.g.* the crossed extension reflex, and it is easy to produce 'fatigue' of the reflex when the reflex is evoked in that way, indeed it seems as easy as when the reflex is provoked from the skin. It may be argued from this that the seat of the fatigue lies less at the peripheral ending of the afferent channel than in the central reflex mechanism itself. In the intraspinal mechanism it can hardly be a phenomenon belonging to that part of the mechanism which as shown above is common to the two afferent channels from the separate receptive points *A* and *B*, since on testing that mechanism through *B* after producing fatigue through *A* little or no sign of fatigue is evident. It seems to me likely that the fatigue is due to a change at the synapse between the afferent neurone, *e.g.* *S* α , Fig. 19, and the next link forward, *e.g.* *P* α , Fig. 19, in the reflex chain. I have already advanced such a view elsewhere².

If the axis cylinder is a fluid conductor (J. S. Macdonald³, Jenkins and Carlson⁴, Carlson⁵), and if other cell-branches which conduct resemble in this respect the axis-cylinder, and if there be not actual continuity of physical phase between the conductive part of one neurone and the conductive part of the next, *i.e.* if there do not exist actual confluence between them, a surface of separation exists between them. Even should a membrane visible to the microscope not appear, the mere non-confluence of the one with the other certifies a surface of separation. A surface of separation constitutes in various physical respects a membrane. The characteristics of reflex-arc conduction, as

¹ *Phil. Trans. Roy. Soc. London*, B. 1897. Also Schäfer's *Text-Book of Physiol.* II. p. 831.

² Schäfer's *Text-book of Physiology*, II. p. 831. 1900; and *Brit. Assoc. Reports*, Address to Section I, Cambridge. 1904.

³ *Proc. Roy. Soc.* 76 B. 1905.

⁴ *Journ. of Comp. Neurol.* xiv. p. 85. 1904.

⁵ *Americ. Journ. of Physiol.* XIII. p. 351. 1905.

distinguished from nerve-trunk conduction, may be referable to that membrane. The conception of the nervous impulse as a physical process (du Bois Reymond) gains in the light of recent physical chemistry. The injury-current of nerve seems comparable in mode of production (Macdonald)¹ with the current of a concentration cell, where a physical process (allied to expansion of a gas) not a chemical provides the energy. Speed of propagation, brevity of time-relations, facile excitation by mechanical means, favouring influence of drying and of cold, absence of detectable temperature change, these are features of nerve-conduction which, as Macdonald² and others urge, argue a physical rather than a chemical basis. A transverse surface of separation, a membrane, in the path of such conduction must modify the conduction. The synaptic membrane would restrain diffusion, bank up osmotic pressure, restrict movement of ions, allow a double electric layer, accumulate electric charges, alter shape and surface-tension with change in potential, alter in potential with change of shape and surface-tension, preserve difference of concentration of electrolytes, and separate colloid suspensions or ion-proteids of different electrical sign. Thus, by such a membrane reversibility of conduction though obtaining in the conductor on either side, might, as Mr Hardy has pointed out to me, be replaced by irreversibility of conduction between one conductor and the next, in virtue of irreciprocal permeability of the membrane. At nexus between efferent nerve fibre and muscle-cell there is, it is generally admitted, no actual confluence of the two cells; there is at their meeting a surface of separation. Here, as also in the conjoined nerve and electric organ, features occur in the reaction that resemble those specially distinguishing reflex-arc conduction from nerve-trunk conduction, though not of such marked degree. In these cases, as also in Beth'e's *Carcinus* experiment, the characteristics are not due to perikarya (nerve-cell bodies), for such are absent. Irreversibility of conduction is met with in the spinal arcs of vertebrates and is not met with in the nerve-net system of *Medusa*, which latter exhibits reversible conduction (Romanes³, Nagel⁴, Beth'e⁵, and others). In *Medusa* microscopic analysis finds (Beth'e, Apathy) the nerve-cells of the net to be actually continuous, *i.e.* obtains no evidence of a surface of separation or membrane at their points of conjunction; a synaptic membrane seems absent there. In the spinal arcs of vertebrates microscopical analysis has on the whole failed to find direct confluence of one neurone with another. The functional indications of the existence of a membrane at the synapse in such arcs are therefore not contradicted but rather supported by histological evidence.

The supposition that at the meeting-place of neurone *A* with neurone *B* a membrane intervenes in the path of conduction, and that prolonged activity of reaction induces a lessening of the conductivity (permeability) of the synaptic membrane in the direction from *A* to *B*, affords a working hypothesis, which although it does not enlighten us much further, seems to meet the facts of reflex fatigue brought forward in this paper.

We may attempt to assign several characters of the scratch-reflex to places in the chain of its reflex-arc. By the method of 'successive

¹ Thompson-Yates, *Laboratory Reports*, Liverpool, III. 1901.

² *Proc. Roy. Soc. London*, 76 B. 1905.

³ *Phil. Trans. Roy. Soc.* 1877 and 1880.

⁴ *Pflüger's Archiv*, LVII. p. 495. 1894.

⁵ *Allgem. Physiol. d. Nervensystems*, Leipzig. 1903.

degeneration¹ it has been shown that long axones descend from cells in the spinal segments of the shoulder and thoracic and lumbar segments, and pass to the spinal segments containing the motor neurones of flexors of hip, knee, and ankle. It was also shown² that these axones in their course along the cord take a path corresponding with that proved³ to be essential for the scratch-reflex. This correspondence renders probable the following as a reflex chain for the scratch-reflex (Fig. 19)⁴; a receptive neurone ($S\alpha$ or $S\beta$, Fig. 19 B) from the skin to the spinal grey matter of the corresponding segment, *e.g.* of the shoulder region. (ii) A long aborally-running propriospinal neurone (Fig. 19, B, $P\alpha$), from shoulder-segment to the grey matter of the hind limb segment. This is the internuncial path. (iii) A motor neurone (Fig. 19 B, FC), from the spinal segment of the leg to the flexor muscles. This last is the *final common path*⁵. The reflex-arc would thus consist of three neurones. It enters the grey matter twice, that is, it has two neuronic junctions, two synapses. It is a disynaptic arc. I venture to express schematically the construction of this arc as disynaptic, but in doing so I am influenced by the desire to express it as simply as possible so far as is consistent with the ascertained data of the case.

The change in the reflex reaction which was above termed fatigue seems on the grounds adduced most probably referable to alteration at a synapse. The spatial restriction of the 'fatigue,' in view of which it was described as 'local,' helps to posit its place in the reflex-arc. Several of the observations given in the foregoing sections indicate that the internuncial path, $P\alpha$ for instance, is common not only to the receptive path $S\alpha$ and to similar afferent paths commencing in the receptive skin field at distances not too widely removed from the point of commencement of $S\alpha$. Among the evidence indicating this is for instance the observation that the refractory phases of the reflex initiated from skin point A applies also to reflexes initiated from skin points B , C , etc., many centimetres distant from A . Also the observation that 'immediate spinal induction' obtains between stimuli at skin point A and stimuli at skin points B , C , etc., several centimetres distant from A .

It might appear that in these effects the neurone FC is the common element answerable for the elision of interference and for the additive

¹ Sherrington and Laslett, *This Journal*, xxix. p. 58. 1903.

² Sherrington and Laslett, *This Journal*, xxix. p. 58. 1903.

³ *Ibid.*

⁴ Sherrington, *Brit. Assoc. Reports*, Cambridge, Addr. Sect. I. 1904.

⁵ Sherrington, *loc. cit. supra*, *Proc. Roy. Soc.* 76 B. p. 269. 1905.

result. That assumption seems contradicted by observations which show that though stimulation of neurone *FC* through a receptive neurone *Sα'* not too distant from *Sα* cannot disturb the refractory phases proceeding under stimulation through *Sα*, yet excitation of *FC* through some other afferent neurones, *e.g.* *L* (Fig. 19 B) of the flexion-reflex, or *R* (same figure) of the crossed extension-reflex, does at once disturb them and sets the rhythmic reflex from *Sα* altogether aside¹. Afferent neurone *Sα'* (a scratch-reflex neurone) therefore must excite *FC* not directly, for if so it is not clear why the phases generated by it should not, like the activities generated by the other receptive neurones *L* and *R*, interfere in *FC* with the phases generated by *Sα*. Receptive neurone *Sα'* must impinge on some mechanism earlier in the chain than *FC*, a mechanism in which refractory phases already established, *e.g.* by *Sα*, cannot be broken through by impulses *viâ* other receptive neurones. Such a mechanism might evidently be the internuncial neurone *Pa*. Therefore the propriospinal neurone *Pa* seems common to receptive paths *Sα* and *Sα'*. This arrangement might be expressed by supposing that receptive neurone *Sβ* of the figure arose in a skin point not too remote from the skin point of *Sα* of the figure, and by representing the internuncial neurones *Pa* and *Pβ* in the figure as each of them common to both *Sα* and *Sβ*. In that case the 'immediate spinal induction' of the scratch-reflex would be explained by *Sα* and *Sβ* both exerting their effects additively on *Pa* or *Pβ* or on both of them.

It then becomes clear that the locus of the above-described fatigue effect must lie on the afferent side of *Pa* and *Pβ*, since that effect unlike the induction can be restricted to either *Sα* or *Sβ*. But much collateral evidence weighs against supposing the seat of the fatigue to lie anywhere along the continuity of the neurone. Its seat should therefore lie at one or both of the neurone-terminals, the peripheral in the skin or the deep in the cord. Some, though not conclusive, evidence argues that the fatigue is not referable, or is not chiefly referable, to the former: there is no evidence that it does not lie, chiefly at least, at the latter. On the contrary it seems inevitable that prolonged activity under prolonged excitation will induce in the synaptic membrane a change unfavourable to conduction. The intraspinal terminal of the receptive neurone is a component in the synaptic membrane of the first synapse of the arc. The seat of the 'local' fatigue is therefore preferably posited in the synapse $\frac{S\alpha}{Pa}$, the first synapse of the disynaptic arc *SαPaFC*. The

¹ Sherrington, *Brit. Assoc. Reports*, Cambridge, *loc. cit.* 1904.

'immediate spinal induction' is on the other hand referred to the inter-nuncial neurone Pa (respectively Pa'). The refractory phase is referable either to Pa (respectively Pa') or to its synapse with FC .

Rapid onset of 'local fatigue' renders it difficult to excite by stigmatic stimulation at one spot of skin a scratch-reflex of more than 80 or 90 beats. On the view, just detailed, that this fatigue has its seat at the first synapse $\frac{Sa}{Pa}$ (or $\frac{S\beta}{P\beta}$) Fig. 19 B, it was thought that more prolonged reflexes might be obtained in the following way, advantage being taken of 'immediate spinal induction.' At each of several, *e.g.* eight, skin points a series of induction shocks is delivered, the shocks of each series falling at their point of application so infrequently that at the intensity used the series at that point is of itself ineffective to excite the reflex. The rate in several of my observations was 18 shocks per 10 secs. But the stimuli thus delivered at each of the eight skin points

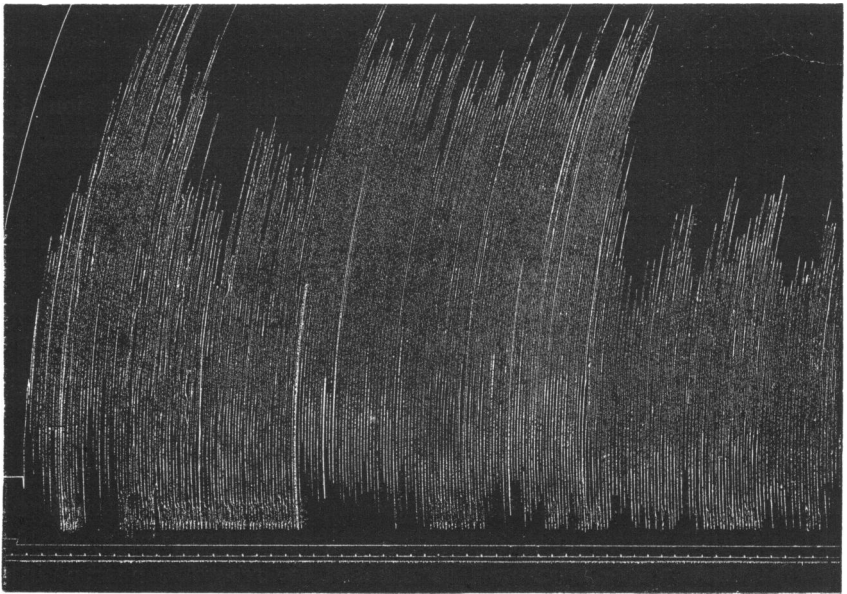


Fig. 23. The scratch-reflex evoked by faradic stimulation in such a way as to obviate local fatigue. The whole reflex of which the figure shows only the first part included a series of 434 beats. The lowest line on the tracing records the delivery of the exciting shocks (double shocks); the next line marks time in seconds, the line third from below is the signal marking the duration of the stimulation.

when taken together for all the skin points as a group succeed each other at the rate of 144 per 10 secs., and are arranged at fairly equal intervals. The skin points at which the eight needle-electrodes are applied are chosen so as to lie each about 4 per cent. from the nearest other one. By positive spatial induction there occurs summation of the eight subliminal series to a series which is supraliminal for the reflex. The result of this arrangement justified the expectation mentioned. Scratch-reflexes of much longer exemption from fatigue are thus obtained (Fig. 23). Some of the reflexes possess series of between 400 and 500 beats. There is here a marked difference from the cell of *Malapterurus*, which yields a series of at maximum only five reflex beats.

With experiments of this form a curious result was met. The series of beats elicited is apt to end not gradually with irregularly enfeebled and very sluggish beats, but abruptly with the sudden occurrence of three or four terminal beats not particularly marked by characters of fatigue. Also, in the course of the long series of beats places of decrement and of some slackening tend to occur, but are recovered from without any full cessation of the reflex. Further, when cessation has actually occurred, if the stimulation although no longer evoking any reflex response is persisted with and maintained unaltered, the reflex response will after a varying interval in my observations from 20 to 70 secs. suddenly reappear and without bearing traces of fatigue. The reflex will then continue for it may be 400 beats or more, again abruptly to disappear, and later suddenly reappear, and again without obvious characters of fatigue. In this form of experiment I have on one occasion applied the stimulus unbrokenly for as long as twelve minutes (the recording paper then giving out) and in that time have seen seven reflexes with long series of beats recur, abruptly subsiding and abruptly reappearing, the last reflex exhibiting 362 beats and still showing none of the ordinary features characterising the 'local fatigue' before described. That the induction shocks were actually applied throughout was certified by their registration on the tracing, as in Fig. 23. The mode of subsidence of the exhibitions of the reflex in such records seems to resemble the mode of subsidence under inhibition.

'Fatigue' of the scratch-reflex occurs earlier with weak excitation than with strong, a result that at first sight seems paradoxical; Fig. 24 illustrates this. The reflex which had ceased to be elicited by the stimulus A was then provoked by increasing the intensity of the stimulus applied by the same electrode as delivered A and at the same skin point. The rate of delivery of the induction shocks remained unaltered but their

intensity was increased. The electro-magnet (top line in the figure) shows the time and duration of the increase of current in the primary by marking larger excursions. The threshold-value of stimulus for the reaction as it rises during the course of the reaction, evidently rises above the value of the weaker stimulus, but the reaction has still a threshold-value of

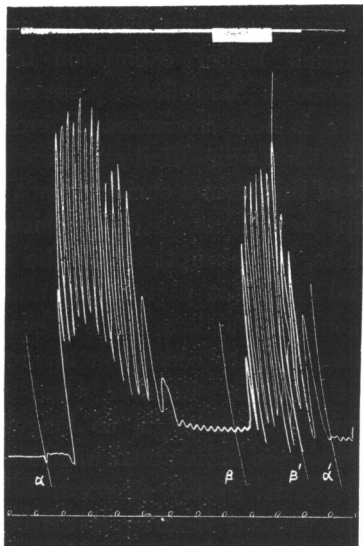


Fig. 24. Fatigue in the scratch-reflex. The duration of faradic excitation is marked above by the broad white line given by the excursions of the electro-magnet with the rapidly repeated current interruptions. The duration of increased intensity of the stimulus is recorded by the still wider excursions of the electro-magnet when its actuating current was increased by removal of 5 ohms from the primary circuit. Time below in secs.

stimulus which the value of the more intense stimulus exceeds. In other words the decline of the reflex under the weaker stimulus is relatively to the production of the motor-discharge greater than under the stronger stimulus.

IX. SPINAL SHOCK.

Immediately on transection of the cord there ensues in the reflex-arcs behind the transection the well-known depression of reaction termed 'spinal shock.' This affects the scratch-reflex more than the knee-jerk, the flexion-reflex, or even than the 'extensor-thrust.' From it the scratch-reflex emerges slowly in the course of weeks or months.

Its time of emergence is in my experience variable. The reflex is at first obtainable only by mechanical stimuli; later as it improves it becomes amenable to electrical. The character of the reflex when obtained in this period is seen in Figs. 25 and 26. The latent period

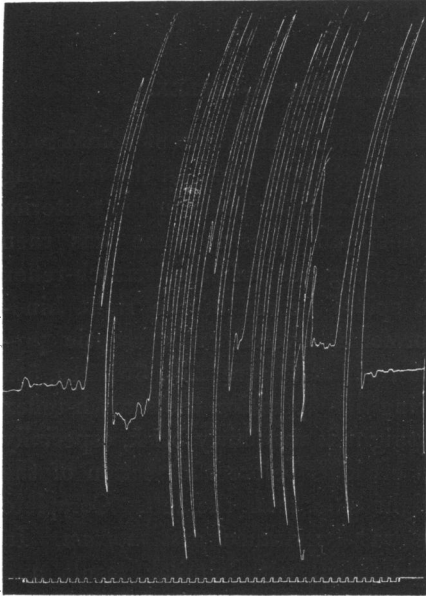


Fig. 25.

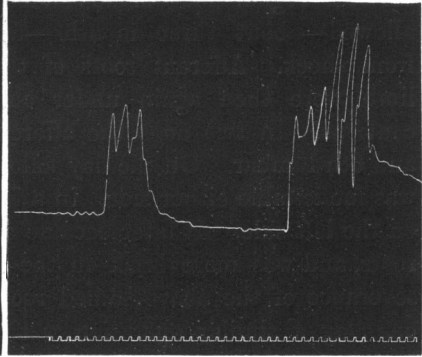


Fig. 26.

Fig. 25. The scratch-reflex in 'spinal shock.' The reflex was inelicitable by faradisation. The time-marker marking fifths of seconds is employed also as signal, and signals the duration of application of the mechanical stimulation. The irregular beats, long latency, and imperfect elicibility of the reflex are seen.

Fig. 26. The scratch-reflex under 'spinal shock.' Similar to foregoing but with the reflex in a deeper state of depression, and under stimulation of a skin point that would give the 'high' form of the reflex. The reflex soon lapses altogether although the stimulation is continued.

is longer than normal, the reflex-response rapidly tires out, the rhythm and amplitude of the beats are irregular, and the beats are sluggish. The instances figured were obtained by the most favourable form of stimulation, namely, the mechanical, and the stimulation applied vigorously during the whole time signalled by the '2" time-marker.

'Spinal shock' has often been regarded as a phenomenon of inhibition (Goltz and others); the character of the scratch-reflex under such shock seems to me to resemble that impressed on it by 'fatigue' rather

than inhibition. The spinal centre seems in a state comparable with a general fatigue. This similarity between the condition of shock and of fatigue, the latter being as said above probably referable to alteration in the synapsis, seems conformable with v. Monakow's¹ explanation of shock as due to a 'diaschizis' in the neurone-chains.

X. APÆSTHESIA AND THE SCRATCH-REFLEX.

The scratch-reflex persists after severance of the afferent spinal roots of the scratching limb itself. This observation is based on the following experiments. In each of six dogs a spinal transection in the posterior cervical region was made under deep anæsthesia; time was then allowed—about three months—for emergence of the scratch-reflex from shock. Afferent roots of the spinal nerves of the right hind-limb were then again under chloroform severed with aseptic precautions. In two dogs the afferent roots cut were 2nd, 3rd, 4th, 5th and 6th lumbar. On the day following this operation the scratch-reflex was inelicitable either side. In a fortnight it was fairly brisk, especially on the left side. It later became as brisk as before the section of the roots, and was more brisk on the right side than the left. Complete severance of the above-named roots was ascertained *post mortem*. In one dog a similar operation was performed with similar result, and a further severance of roots, which proved to be the 8th and 9th post-thoracic, was carried out later. The scratch-reflex reappeared after a short absence subsequent to this latter. In this case therefore all the roots of the limb were divided with the exception of the 7th post-thoracic, which is a large one. In a fourth dog the procedure was as in the last preceding, but at the third operation three roots were severed behind the five previously cut. The scratch-reflex was little interfered with, even temporarily. It was more brisk on the side of the divided roots (apæsthetic) than on the opposite. Its frequency and vigour were fully up to normal, and it was one of the most regularly excitable instances of the reflex that we have ever had in the laboratory. It was less rapidly subject to local fatigue; unipolar faradisation by a stigmatic electrode frequently excited reflexes of 150–180 beats. It was noted that from a small patch of skin at the buttock reflexes of the tail could be elicited; at the *post-mortem* examination the three roots severed at the last operation were found to be the 10th, 8th and 7th post-

¹ *Ergebnisse d. Physiologie, Bio-physik*. 1^{te} Jahrg., p. 563. 1902.

thoracic, the small 9th root having been missed. Suspecting some mistake in the root division I two days before destroying the animal severed under chloroform narcosis, the hamstring nerve at its exit from the sciatic notch; this must have cut any contribution of the afferents from the flexor muscles of the knee which the uncut 9th root may have permitted. The scratch-reflex still persisted, though modified and reduced in its flexion, no doubt owing to the section of the motor nerves to the direct knee-flexors. In a sixth dog after the spinal transection and the recovery of the reflex the afferent roots of the 4th, 5th, 6th, 7th and 8th post-thoracic nerves of the right side were under chloroform anæsthesia severed. The scratch-reflex reappeared after this, and as in the other cases became rather more brisk on the apæsthetic side than on the opposite. Its characters both to inspection and in graphic records resembled the normal spinal reflex.

From this I conclude that the scratch-reflex is not set aside nor even obviously altered by severance of the afferent nerves of the scratching limb itself. The execution of the scratch-reflex seems therefore not dependent on or obviously influenced by centripetal impulses from the muscles that are themselves the field of the reflex contraction. H. E. Hering¹ similarly found the 'wisch-reflex' of the frog, little or not appreciably altered by severance of the afferent spinal roots of the limb that itself executes the movement.

XI. THE SCRATCH-REFLEX AS AN ADAPTED REACTION.

In the spinal dog the scratch-reflex, although vigorous, prompt, and easy to elicit, yet fails to effect the object for which it seems obviously adapted, namely to scratch the skin whose irritation evokes it. The scratching paw is, as said above, directed roughly toward the point irritated, and if that point lie farther headward the paw is carried farther headward, if farther backward is brought farther backward, and so on. But the point irritated is in my experience never actually reached. Not only that but in many instances the scratching paw does not reach the receptive field of skin anywhere. By laying the animal gently over so that the weight of the limb tends to help its flexion, and then eliciting the reflex it may be contrived that the scratching paw does reach the receptive skin field, though not usually at the point first irritated. The reflex then supplies its own stimulus, and, since

¹ *Archiv f. exper. Pathol. u. Pharmak.*, Leipzig, xxxviii. p. 266. 1896.

the paw wanders a good deal in its contact with the receptive skin from moment to moment, the total reflex resulting is sometimes very prolonged, although irregular (Fig. 27).

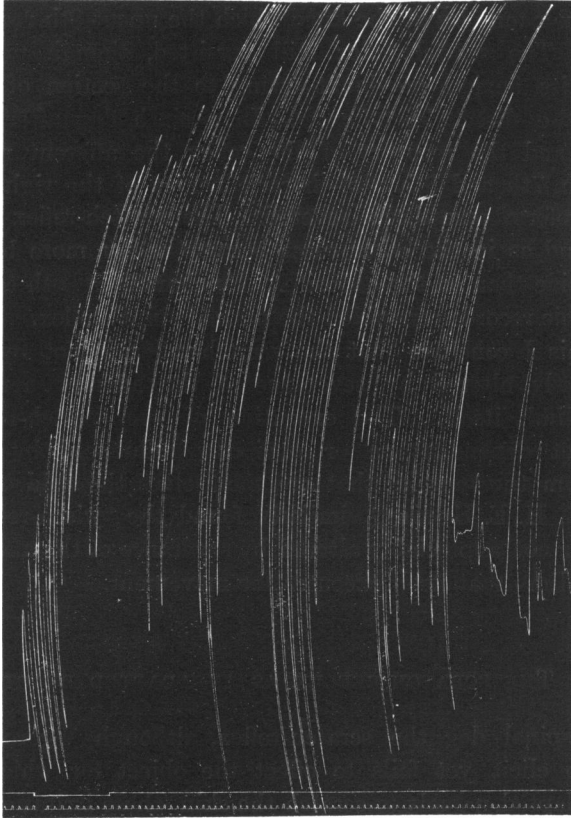


Fig. 27. The scratch-reflex initiated by an electrical stimulation and then self-maintained by the excitant action of the scratching foot on the receptive skin field. Time below in $\frac{1}{100}$ th secs. The signal line marks the duration of the electric stimulation.

The reflex is presumably adapted to act against the parasitic life which makes the hairy coat a habitat. It is difficult to judge in what way and to what extent the scratching movement avails against the attacks of parasites. I have been quite unable to satisfy myself that the movement really combs the parasite out. It may be that the movement causes some reflex in the parasite which inhibits the insect from biting further. Also it seems probable that the scratching allays the irritant sensation in the attacked skin.

The tickling touch yielded markedly by the skin near the alæ of the nose in ourselves is rapidly allayed by rubbing the skin there. v. Frey¹ suggests this tickling is brought about by vaso-motor changes induced by the touch. It may be supposed that in the dog the cutaneous nerve-endings which acting simply as receptive organs evoke the scratch-reflex evoke as sense-organs sensations of an itching kind. Since there is a general correspondence between a reflex reaction and a sensual reaction when both are induced through one and the same receptive apparatus, a broad likeness may be taken to hold between the reaction of the scratch-reflex and its concomitant itching sensation, although the latter is probably not so rhythmic. A salient feature of the scratch-reflex when studied as a purely spinal reaction is the rapidity with which it subsides and wears out, the above-mentioned 'local fatigue.' It does not seem strained to imagine that with the subsidence of the reflex its concomitant itching sensation also subsides. The 'fatigue' which, as was shown above, there seems reason to posit at the first synapse would in that case not only bring about subsidence of the reflex movement but might also cure the irritation which excited that reflex movement if the same or a similar synapse joined the cerebral path.

It is not obvious why so extensive a reflex mechanism should exist for suppressing these cutaneous irritations, which though doubtless frequent are not very intense and might be supposed of little relative importance to the organism. Viewed broadly the scratch-reflex is but one example of a widely spread class of reflex reactions that are adapted to preen and preserve from irritation the tegumental surface. Other examples of the class are the cleansing movements of the 'spinal' fly and grasshopper and crayfish, etc., the 'wisch-reflex' of the spinal frog, the 'nettoyage' of the tortoise (Bickel)², the 'shake-reflex' of the spinal dog, the panniculus carnosus reflex of the horse, and the conjunctival reflex also, in the broad sense a segmental skin-reflex. One advantage probably secured by these reflexes is the freeing of the receptive surface from insignificant stimuli, and thus keeping it a clean slate, so to say, for fresh stimuli to write on. When then a significant stimulus does arrive its excitation ensues unconfused with concomitant registration of multitudinous other excitations of little or no significance to the organism.

¹ *Sitzungsb. d. k. Sächs. Gesellsch. d. Wiss. z. Leipzig.* 1894.

² *Rev. méd. d. l. Suisse romande, Geneva.* 1897.

SUMMARY OF CONCLUSIONS.

1. In the scratch-reflex a spinal mechanism replies rhythmically, with little variance of rhythm, to stimuli whether constant and continuous or rhythmic. With rhythmic stimuli the frequency of the rhythm of the stimulation is immaterial to that of the reflex so long as the stimulation is able to excite the reflex at all.

2. There is, therefore, rhythmic recurrence of a refractory phase in the reaction of the scratch-reflex arc. The rate of recurrence is on the average about 4.8 times per sec. in the spinal dog.

3. The refractory phase is profound in its degree of refractoriness; so far as tried, stimuli even the most intense altogether fail to break it down.

4. In the above characters the scratch-reflex closely resembles the swimming-beat of *Medusa*—and the rhythmic action of the heart. But the scratch-reflex does not present the ‘all or nothing’ phenomenon. On the contrary it presents in high degree the feature—little present in certain spinal reflexes and denied to spinal reflexes in general by various authorities—of graded intensity of contraction in response to graded intensity of stimulus.

5. The efferent mechanism of the reflex is knit together intraspinally so as to form a fairly unitary whole. Hence a reflex employing the full intensity of action of the efferent mechanism can be discharged by excitation of any single spot in the receptive field, subject only to the reservation that the threshold value of stimulus is not the same for all points in the receptive field. Hence, further, stimuli applied at separate points in the field exert not only a summed action, but a mutual influence of facilitation and reinforcement the one on the other. The element in the reflex arc in which this summation and ‘bahnung’ have their seat is probably the internuncial neurone (Pa , Fig. 19).

6. The refractory phase has its origin in an intraspinal mechanism between central end of afferent (receptive) neurone and central end of efferent (motor) neurone. Probably this mechanism is the descending propriospinal neurone Pa (Fig. 19) internuncial between Sa and FC or the synapse between Pa and FC .

7. Each such internuncial neurone seems to receive impulses from many receptive neurones, and to be common to receptive neurones, not only of one spinal segment, but of several.

8. The final efferent neurones (motor root neurones) engaged in the rhythmic discharge of the reflex seem all of them open to impulses from all the receptive neurones in common. Both the internuncial and the final efferent paths are therefore 'common paths,' but the final path exhibits a higher degree of community than the internuncial.

9. The receptive skin-field of the scratch-reflex is an area of origin of reflex-arcs (scratch arcs) the mutual relation of which, one to another, is that of 'allied arcs,' that is, their reactions exhibit harmonious, facilitating and reinforcing relationship in regard to a '*final common path*.'

10. The scratch-reflex as elicited from one part of the receptive field is not fully the same as when elicited from some other part of the field. The scratch-reflex is therefore really a reflex type comprising individual reflexes of more or less close similarity. The greater the likeness between any two of the component reflexes the greater the mutual facilitation and reinforcement exhibited between them.

11. The receptive field of a reflex, *e.g.* scratch-reflex, offers to stimuli a threshold which is of very different value at different parts of the field. The absolute values vary much even from day to day in the same spinal animal, but the relative values are much less variable.

12. The scratch-reflex when evoked from any single spot in the receptive field rapidly subsides even under continued application of the stimulus. This subsidence may be regarded as a form of 'fatigue': it is a phenomenon of localised distribution, being closely restricted to the particular reflex arcs arising in the spot of skin actually under excitation.

13. This fatigue is not referable to the internuncial and final efferent neurones of the reflex-arc. Analysis points to its being due to changes at the junction between the afferent neurone and the internuncial neurone, that is, to alteration in the synaptic membrane of the first synapse, *e.g.* $\frac{S\alpha}{P\alpha}$ (Fig. 19) of the reflex-arc.

14. By exciting the reflex discharge by slight stimulation of a number of different receptive neurones the 'fatigue' should be avoidable and more prolonged reflex discharges be obtainable: experiment finds this to be the case, and reflexes exhibiting series of 500 beats result.

15. The 'after-discharge' of the reflex is rhythmic and characteristic, though not so extensive as in some reflexes. It increases with intensity of the reflex reaction, *e.g.* under intense stimuli. Fatigue diminishes it: so also does 'spinal shock.'

16. The latent time of the scratch-reflex is relatively to that of several other spinal reflexes peculiarly long. Its duration is shortened by intensifying (or, with a rhythmic stimulus, increasing the frequency of) the stimulus. Its duration is lengthened by weakening the stimulus, and under fatigue, and 'spinal shock.'

17. 'Spinal shock' as judged from the scratch-reflex resembles a deep general fatigue rather than a condition of inhibition.

18. The severance of the afferent roots of the scratching limb itself far from impeding or impairing the scratch-reflex renders it more brisk and leaves it unaltered in rhythm.

19. In the 'spinal' dog even with the best recovery of the reflex in regard to facility and intensity of excitability, its accuracy in the directing of the foot to the irritated point remains extremely defective. This ataxia in regard to 'local sign' seems traceable less to defective adjustment of the clonic component of the reflex contraction than to that of the tonic component.

20. It is not clear how the scratch-reflex considered as an adapted reaction arrives at relieving the sentient surface. It acts perhaps by causing rapid and brief lasting local extinction of the responsiveness of the surface at the seat of irritation.

21. A rhythmic crossed stepping-reflex is elicitable by faradic stimulation of the hind foot of the spinal dog: the rhythm of this reflex is about twice as slow as that of the scratch-reflex.